SEASONAL CYCLES OF TWO SPECIES OF SCALLOP (BIVALVIA: PECTINIDAE) ON AN INSHORE AND AN OFFSHORE FISHING GROUND.

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor of Philosophy

by

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Dedicated to the memory of my ever loving family
(1917-1989)

W.M.P.B. Wanninayake (father)

B.M.B.M. Wanninayake (mother)

W.M.U.B. Wanninayake (brother)

W.M.K.B. Wanninayake (brother)

W.M.S.K. Wanninayake (sister)

for showing me the way of life

and showing me its value.

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Seasonal cycles of two species of scallop (Bivalvia: Pectinidae) on an inshore and an offshore fishing ground.

W.M.T.B. Wanninayake

ABSTRACT

Seasonal cycles of reproduction, energy storage and energy utilisation were investigated over a period of two years (May 1991 to April 1993) in two commercially exploited species of scallop: the queen scallop *Aequipecten opercularis* and the great scallop *Pecten maximus*. Population of each species from two areas with differing environmental conditions were selected for comparative study, namely an inshore (Laxey Bay) and an offshore (10 nautical miles (18.5 km) south east of Port St. Mary) fishing ground. Three aspects relating to the reproductive biology were studied. Firstly, the annual spawning cycle of both species was assessed more precisely than in previous studies. Secondly, changes in somatic tissues were observed, in relation to reproductive events, in order to describe the fate of each body component during gametogenesis. Finally, seasonal cycles of energy storage and utilisation in different somatic tissues were investigated.

For *Aequipecten opercularis* there were three more-or-less distinct peaks of spawning each year in the Laxey Bay population (winter, summer, autumn) but only two in the Port St. Mary population (winter, summer). For *Pecten maximus* there were two peaks in the Laxey Bay population (summer, autumn) but only a single summer peak in the Port. St. Mary population. The most important spawning period of both species was in the summer but there was probably also some continuous low-level release of gametes throughout the spring and summer. In the smaller number of annual spawning peaks and the absence of an autumn spawning, the offshore Port St. Mary populations resembled other populations further north in the geographical range, for both species. In contrast, the spawning patterns of the Laxey Bay populations were generally similar to those described for other Irish Sea and more southerly populations.

There were distinct seasonal cycles in the dry weight of the somatic tissues (adductor muscle, mantle tissue, digestive gland, gonads) and in their biochemical composition (protein, lipid, glycogen) for both species. The dry weight of the adductor muscle was lowest in spring but increased during the summer to a maximum in autumn. This was due primarily to an increase in protein and glycogen. The digestive gland followed a similar seasonal pattern but changes in weight also involved large changes in lipid. Mantle tissue varied little seasonally but followed the same pattern. Seasonal cycles of dry weight and biochemical composition of the gonads were the inverse of the cycles in the other tissues, rising through autumn and winter to a high level in spring, then falling through the summer. Major variations in biochemical composition of the gonads were due mainly to protein and lipid, these being the major constituents of the gametes.

Gametogenesis of both scallops and queens took place mainly during the winter, when food availability is low. It was supported by reserves of protein and glygogen stored mainly in the adductor muscle, and lipids stored mainly in the digestive gland. These nutrient reserves also supply maintenance energy demands during the winter. The quantity of lipid lost from the digestive gland was adequate to account for that built up in the gonads but specific amino acids may be synthesised from glycogen.

The seasonal cycles of both species differed in magnitude and timing on the two grounds. Nutrients built up to higher levels in the Port St. Mary populations and with no autumn spawning in either species on this ground, gametogenesis and the depletion of stored reserves proceeded 1-3 months earlier than in the Laxey Bay populations.

The synchronisation of seasonal cycles, and the differences noted between the two species and between the two gounds, are discussed in relation to various environmental factors including phytoplankton productivity, temperature, depth, water currents and other hydrographic features. The genetic regulation of spawning cycles is also discussed and areas for future research are highlighted.

GENERAL INTRODUCTION

The scallops, of the family Pectinidae, are economically important bivalves in many parts of the world. Generally the only parts eaten are the adductor muscle and sometimes the gonads. There have been about 400 living species of scallops identified so far, in marine waters from polar regions to the tropics. Commercially exploited species are mostly found in high latitudes between 30° and 55° in both northern and southern hemispheres (Brand, 1991).

The great scallop, *Pecten maximus* (L.) and queen scallop or queenie, *Aequipecten opercularis* (L.), which are mainly distributed in the eastern North Atlantic region (Tebble, 1966; Broom, 1976; Mason, 1983; Piccinetti *et al.*, 1986), have a high market value. Both species are common in water depths of 20 - 45m with bottoms of clean firm sand or fine gravel (Mason, 1983; Duggan, 1987; Brand, 1991).

The main fishing grounds for these two species are around the British Isles and off the coasts of France namely; Baie de Brieuc, Baie de la Seine, eastern and western English Channel, all around the Isle of Man, the Clyde Sea, west of Kintyre, Orkney, Shetland, Moray Firth and several places in the North Sea (Ursin, 1956; Rolfe, 1973; Mason, 1983; Sinclair *et al.*, 1985). Owing to irregular recruitment and overfishing in European waters, stocks of these two species have become depleted in the last two decades (Dupouy & Latroite, 1976; Brand *et al.*, 1980; Mason, 1983; Duggan, 1987; Paul, 1987; Allison, 1993). Therefore various research programmes have been carried out in this period to improve management strategy (Gibson, 1956; Duff, 1976; Hancock, 1979; Mason, 1983; Allison, 1993), and to develop and implement aquaculture and

restocking (Comely, 1972; Mason & Drinkwater, 1978; Paul, 1978; Brand *et al.*, 1980; Ventilla, 1977, 1981; Murphy, 1986; Whittington, 1993).

A knowledge of the spawning cycle of bivalves may be important for various reasons. For commercial purposes it is often essential for conservation and management decisions, for collection of spat, conditioning and spawning, and maintenance of culture materials (Gutsell, 1930; Barber & Blake, 1991). Much of a species' life history and biology will remain obscure until this period is determined (Gutsell, 1930).

The changes in the weight of various tissues in the body mainly relate to the spawning cycle of the animal (Sastry, 1979). This situation is especially important in pectinids, because their weights (comprising mainly the adductor muscle and gonad which are the commercially saleable parts) vary seasonally with the spawning cycle (Mason, 1958a; Stanley, 1967; Comely, 1974; Soemodihardjo, 1974; Connor, 1978; Barber & Blake, 1981; Mackie, 1986; Duggan, 1987).

Sexual reproduction of marine bivalves is a cyclical biological and physiological process. They reproduce annually, semiannually or continually through the year (Sastry, 1975). The patterns of reproductive periodicity show a relationship to the environment in which they live (Crisp, 1957). In a seasonally changing environment, the timing of the breeding period is adaptive, spawning occurring when conditions are optimal for development and growth of offspring (Sastry, 1963, 1966a).

Over the last few decades much research has been carried out to investigate the reproductive biology of bivalves from various parts of

the world. Therefore several reviews of research on molluscan reproduction presently exist. Fretter & Graham (1964) reviewed reproduction in the entire phylum Mollusca. Purchon (1977) concentrated on freshwater bivalves and Seed (1976) reviewed reproduction in Mytilidae. Sastry (1979) prepared a comprehensive review of reproductive biology and physiology in bivalves (Pelecypoda) excluding the Ostreidae. Andrews (1979) reviewed various aspects of the reproductive biology of Ostreidae. Mackie (1984) summarised molluscan reproductive biology in both marine and freshwater environments. The annual reproductive cycle of pectinids (as with other marine bivalves) includes the following stages: a vegetative phase, differentiation, cytoplasmic growth, vitellogenesis (maturation), spawning and resting (Mason, 1958a; Giese, 1959a, 1976; Sastry, 1966a, 1966b, 1975, 1979; Naidu, 1970; Giese and Pearse, 1974).

In a single population, pectinids tend to develop and spawn within a limited period, although there are inter and intra-specific differences in the timing (Nicholson, 1978; Mason, 1983; Duggan, 1987) and duration of spawning (Lubet, 1959; Naidu, 1970; Nicholson, 1978; Miller *et al.*, 1979). Environmental differences between years and between habitats cause some variations in gametogenic cycles within a species (Barber & Blake, 1991). In pectinids such as *Pecten novaezelandiae* (Tunbridge, 1968; Bull, 1976), *Argopecten irradians* (Barber & Blake, 1983) and *Pecten alba* (Sause *et al.*, 1987) it has been found that gametogenetic events are very consistent in time each year. The timing of spawning activity differs more between years for *Pecten maximus* (Mason, 1958a, Duggan, 1987), *Aequipecten opercularis* (Soemordihardjo, 1974; Paul, 1978; Duggan, 1987), *Placopecten magellanicus* (Naidu, 1970) and *Chlamys varia* (Lubet, 1959).

Gametogenic cycles vary between locations for *Chlamys varia* (Lubet, 1959), *Aequipecten opercularis* (Ursin, 1956; Duggan. 1987), *Pecten maximus* (Paulet *et al.*,1988) and *Argopecten irradians* (Bricelj *et al.*, 1987a). Some pectinids show differences in gametogenetic cycles due to the water depth (Tunbridge, 1968; Skreslet & Brun, 1969; Skreslet, 1973; MacDonald & Thomson, 1986; Barber *et al.*, 1988). Studies on some pectinid species (*Argopecten irradians, Placopecten magellanicus*) have shown that their reproductive cycles differ in many aspects, such as the timing of gametogenesis, duration of the spawning period, oocyte diameter and fecundity (Belding, 1910; Gutsell, 1930; Reddiah, 1962; Hennick, 1970; Barber & Blake, 1981, 1983; Barber, 1984 and Taylor & Capuzzo, 1983). A number of other factors such as temperature, quality of food, particle size, filtration rate and tidal level may influence food consumption, digestion and assimilation in tissues (Wakui & Obara, 1967; Bull, 1976; Heald & Caputi, 1981; Fuerte & Baez, 1993). Therefore the adaptation to the environment and the organisms' energetics may influence the timing of gametogenesis (Sastry, 1979).

The seasonal cycles of *Aequipecten opercularis* and *Pecten maximus* are similar to other pectinids (Amirthalingam, 1928; Tang, 1941; Mason, 1958a; Soemodihardjo, 1974; Paul, 1978). The major spawning season differs from area to area in term of number of gametes released (Gibson, 1956; Mason, 1958a; Baird, 1966; Stanley, 1967; Duggan, 1987). The timing of spawning is not generally closely synchronised in all individuals in the population and there may be considerable temporal and spatial variation in the timing of spawning period (Comely, 1974; Mackie, 1986).

The seasonal cycle of these two species has been studied by many investigators in European waters, mainly in the United Kingdom, France, and Denmark (Fullarton, 1889; Dakin, 1909; Amirthalingam, 1928; Mason, 1953; Aravindakshan, 1955; Comeley, 1974; Soemordihardjo, 1974; Paul, 1978; Taylor and Venn, 1979; Faveris, 1987; Lubet *et al.*, 1987a, 1987b; Lubet *et al.*, 1991).

For determining the reproductive status of bivalves there has been common use of similar methods such as the subjective staging method (gross observation) (Dakin, 1909; Belding, 1910; Amirthalingam, 1928; Choat, 1960; Soemodihardjo, 1974; Bull, 1976; Nicholson, 1978; Paul, 1978; Heald & Caputi, 1981), microscopic observation (Mason, 1958a; Reddiah, 1962; Naidu, 1970; Bull, 1976; Jones, 1981; Brousseau, 1987; Corni & Cattani, 1990), gonad weight (Taylor and Venn, 1979; Dredge, 1981; Sundet & Vahl, 1981), gonadosomatic index (Sastry, 1966b, 1970a; Duggan, 1987; Lubet *et al.*, 1987a; Sause *et al.*, 1987 Wolff, 1987), or an index relating gonad weight to shell height (Burnell, 1983; Mackie, 1986; Wilson, 1987b). Steriological techniques have been used by Lubet (1959), Nicholson (1978), Llana & Aprieto (1980), Lauren (1982), Taylor & Capuzzo (1983), Mackie, 1986; Wilson (1987b) and Steingrimsson (1989); larval abundances by Fullarton (1889), Gutsell (1930) and Wolff (1987, 1988), and spat abundances by Nicholson (1978), Brand *et al.*, (1980), Burnell (1983) and Wolff (1987, 1988).

Series of investigations have been made to determine the seasonal cycle of storage and utilization of food reserves in bivalves, as gamete production ultimately depends on energy derived from stored nutrients (Giese, 1966, 1969; Gabbott, 1976; Sastry, 1979). The kind of substrates, storage tissues, and the time of utilisation related to reproduction varies

between species as well as between populations of the same species (Sastry, 1979; Bricelj *et al.*, 1987a, 1987b).

A large amount of literature exists on seasonal changes in tissue weights and biochemical composition in bivalves (Ansell & Trevallion, 1967; Giese, 1966, 1969; Walne, 1970; De Zwaan & Zandee, 1972) but few studies have related energy storage and utilisation to pectinid reproductive events (Sastry, 1979; Barber & Blake, 1981; Mackie, 1986). Lopez-Benito (1956) and Barber & Blake (1981) studied the seasonal cycle in biochemical composition with reference to the gonadal cycle, and the cycle of storage and utilisation of reserves in adductor muscle and in other tissues of *Pecten jacobeus* and *Argopecten irradians concentricus* respectively. The spawning cycles of *Pecten maximus* (Comely, 1974), *Aequipecten opercularis* (Taylor & Venn, 1979) and *Chlamys septemradiata* (Ansell, 1974b) are closely related to seasonal changes in biochemical composition and the weights of the soft tissues. Gabbott (1975) for *Mytilus edulis*, Adachi (1979) for *Tapes philippinarum* and Pollero *et al.*, (1979) for *Chlamys tehuelcha* also studied energy reserves in relation to spawning events.

The work presented in this thesis covers some similar areas to previous studies (Aravindakshan, 1955; Mason, 1958a, 1958b; Soemodihardjo, 1974; Paul, 1978; Duggan, 1987) as well as certain previously uninvestigated aspects of the reproductive biology of *Aequipecten opercularis* and *Pecten maximus* in Manx waters.

The first part of the study was directed towards assessing the annual spawning cycle of both species more precisely than in previous studies by carrying out a comparative study of the two species, taken from two areas

where environmental conditions differed, namely an inshore and an offshore fishing ground. The second aim was to observe the changes of somatic tissues in relation to the reproductive cycle of the two species, and to describe the fate of the each body component during gametogenesis. The third part was to investigate the seasonal cycle of energy storage and utilisation during the annual gametogenesis period. It was hoped that the results of these three parts of the study could be combined to predict more precisely the reproductive behaviour of the two species: such knowledge could strengthen the future management of the fishery.

CHAPTER 1

A STUDY OF THE SPAWNING CYCLES OF *AEQUIPECTEN OPERCULARIS* AND *PECTEN MAXIMUS* FROM THE LAXEY BAY AND PORT ST. MARY FISHING GROUNDS IN THE NORTH IRISH SEA

1.1 INTRODUCTION

The seasonal spawning cycles of pectinids in Manx waters have been much studied over the last few decades (Mason, 1958a, 1958b; Reddiah, 1962; Soemodihardjo, 1974; Paul, 1978; Duggan, 1987).

Reddiah (1962) studied sexual differentiation of various pectinid species. Some pectinids, namely *Chlamys striata* (Muller) and *Chlamys tigerina* (Muller) are dioecious, with individuals either male or female throughout their life. *Chlamys distorta* (Da Costa) and *Chlamys varia* (L.) are hermaphroditic but with separate phases and are capable of changing sex. The commercial species *Aequipecten opercularis* and *Pecten maximus* are both simultaneous hermaphrodites with the gonad containing a proximal creamy-coloured male portion and a distal orange-coloured female portion.

Dakin (1909) first described the histological structure as well as the spawning cycle of *P. maximus*. Mason (1958a) carried out a more detailed study of the spawning cycle of *P. maximus*, using both subjective staging and histological methods. Murphy (1986) observed regional variations of the spawning cycle of *P. maximus* on various fishing grounds around the Isle of Man. Aravindakshan (1955) and

Soemodihardjo (1974) described the histological structure and used staging methods to study development of the gonad of *A. opercularis* and Paul (1978) also subjectively assessed the development of the gonad in this species. More recently, Duggan (1987) used both subjective and objective methods for determining the development and spawning cycles of both *P. maximus* and *A. opercularis* in association with a study of spat settlement. Allison (1993) observed the breeding cycles of both species on different fishing grounds by using staging methods.

In the present study, the spawning cycle of *A. opercularis* and *P. maximus* was followed on two different grounds in Manx waters. Three methods were used to assess the spawning cycle: a subjective staging method and two objective methods namely, the gonadal index and gonad dry weight. This enabled a more detailed comparison to be made of these methods.

1.1.1 Staging method

This method was used to assess the reproductive state through gross visual examination and was that most commonly applied by previous workers. However, the stages used to study the condition of the gonad of bivalves vary from one researcher to another, although the fundamental principles are the same (Amirthalingam, 1928; Tang, 1941; Gibson, 1956; Mason, 1958a; Reddiah, 1962; Naidu, 1970; Soemodihardjo, 1974; Paul, 1978; Murphy, 1986; Duggan, 1987; Allison, 1993). The reproductive state of each individual was assigned to one of five stages based on the external appearance of the gonad. The main advantage of this method is that it is the simplest and quickest method of assessing gametogenesis

and large samples can be assessed rapidly in order to gain an overall picture.

1.1.2 Gonadal index

In this method, gonad weight is related to the variation of somatic tissue weight throughout the period. A seasonal reproductive cycle is a distinctive part of most animal species, especially those inhabiting temperate latitudes (DeVlaming *et al.*, 1982). These reproductive cycles are reflected by clear variations in gonad size. When assessing gonadal activity, animals of different sizes are frequently sampled and it is generally assumed that gonad weight depends on animal size and stage of gonad development (Schick *et al.*, 1988). The most common means of accounting for the effect of differential body size on gonad size has been to express gonadal weight as a percentage of the body weight of an individual. This ratio is named the gonadal or gonad index and is widely used as an index of gonadal activity and spawning preparedness. It is also commonly used for comparing groups of animals taken at different times or in different habitats (Sastry, 1966b, 1970a; Skreslet & Brun, 1969; Shafee & Lucas, 1980; Duggan, 1987; Wolff, 1987, 1988).

1.1.3 Gonad weight

This method relates directly to the behaviour of the gonad during the reproductive cycle. The seasonal variation of gonad weight fluctuates comparatively more than any other tissue owing to the growth and subsequent release of gametes. The determination of mean dry weight is more accurate because, for the wet weight, a large amount of water is retained in the lumen of spent and developing gonads (Mason,1958a;

Soemodihardjo, 1974; Taylor & Venn, 1979). This method is useful for assessing gonad development as well as for quantitative estimation of fecundity throughout the spawning season (Ansell & Trevallion, 1967; Sastry, 1966a; Thompson & MacDonald, 1990). Therefore, by using these three methods on the same samples, it was hoped to establish more precisely the times of peak spawnings of both *A. opercularis* and *P. maximus* from the two fishing grounds and to relate this information to environmental factors.

1.2. MATERIALS AND METHODS

1.2.1. Sampling areas

Monthly samples of *Aequipecten opercularis* and *Pecten maximus* were collected over a period of two years, extending from May 1991 to April 1993, by R.V. Roagan from two areas in the Irish Sea (Fig. 1.1). The first area is Laxey Bay (54° 15.5′ N; 04° 22.7′ W) off the east coast of the island at a depth of 20-30 m with a coarse gravel, sand bottom (Jones, 1951; Murphy, 1986). This was considered to be an inshore area, being approximately 6 km from the coast. The second area is about 10 nautical miles (18.5 km) south east of Port St. Mary (53° 50.3′ N; 04° 35.5′ W) at a depth of 50 - 70 m and was considered to be an offshore area. This has a coarse sand, stones and shell bottom (Murphy, 1986).

1.2.2. Sampling procedure

Two types of spring tooth-bar dredges were used for the collection of queenies and scallops. The dredge descriptions are shown in Table 1. 1.

Table 1.1. Specifications of dredges used on R.V. Roagan for sampling *Pecten maximus* and *Aequipecten opercularis* in the Irish Sea.

Dredge type	No. of dredges	Dredge width	No. of teeth	Tooth spacing	Tooth length	Belly ring diameter
Queen	4	76.2 cm	10	7.6 cm	7.6 cm	5.7 cm
Scallop	4	76.2 cm	9	8.6 cm	11 cm	7.0 cm

Four tows of approximately 2 nautical miles (1 nautical mile = 1852 m) were made at each site for the collection of the animals.

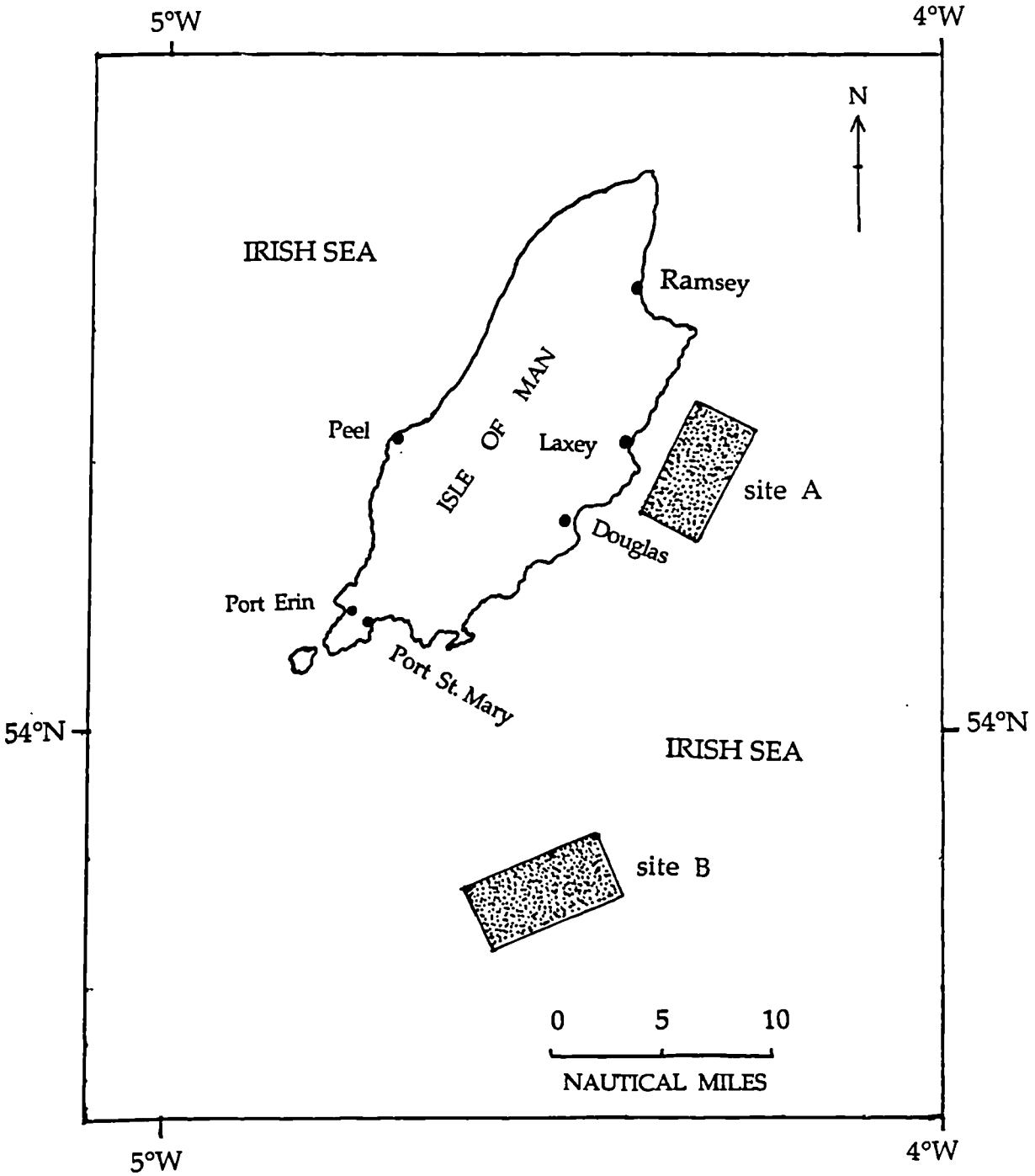


Fig. 1.1. A map of the Isle of Man showing the two sample sites in the Irish Sea (site A = Laxey Bay, site B = Port St. Mary).

The scallops and queenies were separated from the other material and transported to the laboratory in seawater containers. The animals were transferred to running seawater tanks with aeration and left for 24 hours. After cleaning the following measurements were made to the nearest millimetre for both species, using a measuring board (Fig. 1.2).

1. Shell length (anterior-posterior axis)
2. Shell height (dorso-ventral axis)
3. Shell thickness

Both species were aged by counting the number of growth rings on the shell.

For the subjective staging method, the gonad stages defined by Mason (1958a), Reddiah (1962) Naidu (1970) and Soemodihardjo (1974) were considered to be the most convenient for this study and hence were adopted. These authors assign the gonads to one of eight developmental stages, based on external appearance. In the present study no juvenile animals were investigated so gonad condition was divided into only five stages which were termed 'spent', 'recovering', 'filling', 'half-full' and 'full' (corresponding to stages III - VII of Mason (1958a)). The criteria used to define each stage are given in Table 1. 2. Using this method the stages 'spent' and 'full' are easily defined but the remaining three stages are more arbitrary. For details of the histological structure of these stages of gonad development reference should be made to Aravindakshan (1955), Mason (1958a), Reddiah (1962), Naidu (1970) and Soemodihardjo (1974). The gonad stages used in *P. maximus* (stages III -VII) and *A. opercularis* (stages III - VII) are showed in Fig. 1. 3.

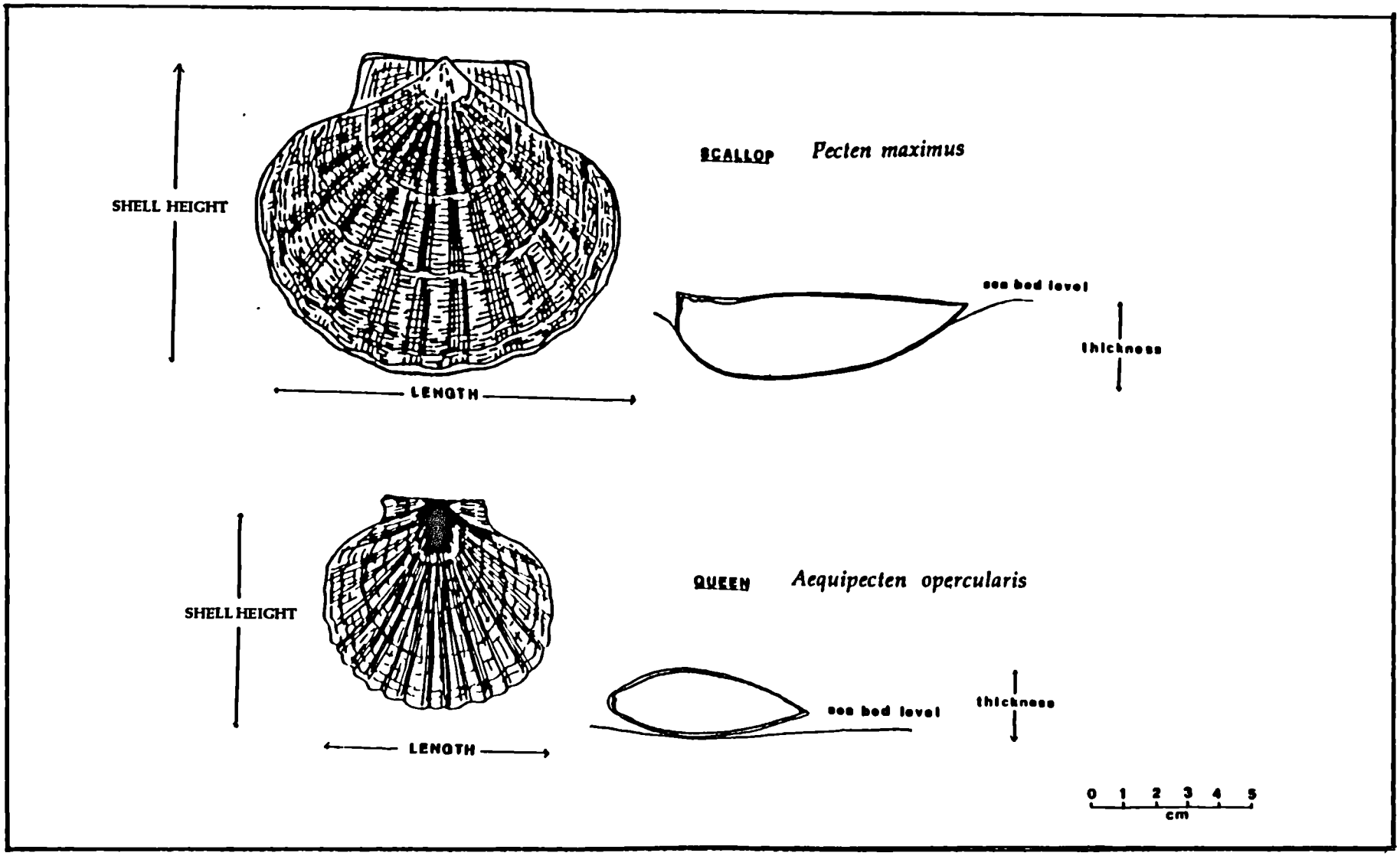
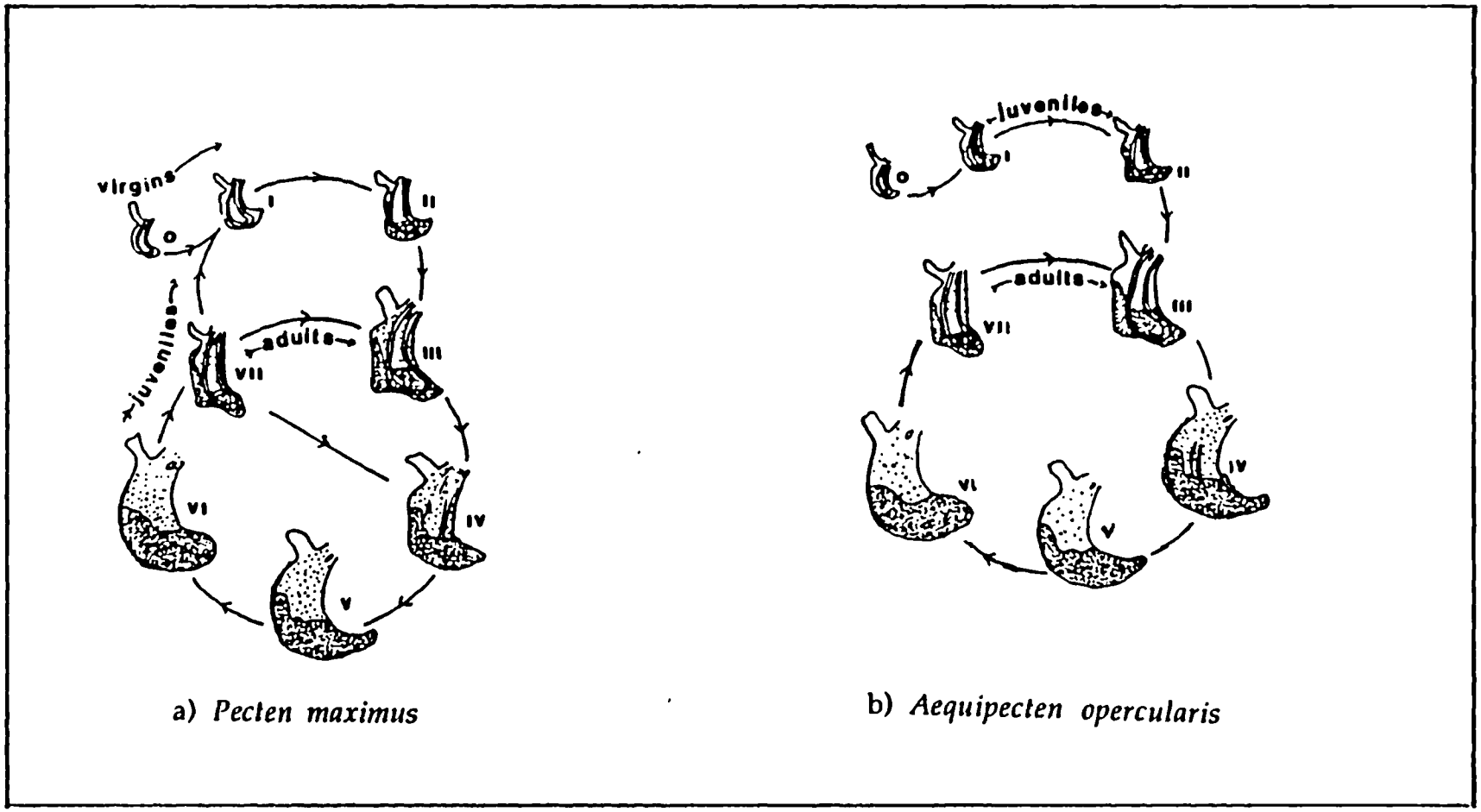


Fig. 1.2. The linear shell dimensions of the scallop, *Pecten maximus* and the queen, *Aequipecten opercularis* (after Mason, 1983).

Table 1. 2. Description of stages used for assessing gonad development of *Aequipecten opercularis* and *Pecten maximus*.

Stage of development	External features
Spent	Gonad usually small, flabby, colourless and containing much free seawater. Differentiation of the male and female portions may not be clearly visible. Loop of alimentary canal can be seen clearly.
Recovering	First evidence of ovary or early development of sperm. Gonad small but thicker, tip pointed. Distal ovary assumes a red colour, proximal testis milky- white. Follicles not densely packed and gonad opaque. Alimentary canal visible.
Filling	Gonad larger, cross section area oblong, tip pointed. Ovary bright red,(*Pecten maximus* - orange) testis milky- white. Follicles closely packed. Alimentary canal sometimes partly visible.
Half-full	Gonad larger, oval in cross section. Bright-red (*Pecten maximus* - orange) with pointed tip. Testis creamy -white. Follicles closely packed. Alimentary canal not visible.
Full	Gonad very large bright-red,(*Pecten* orange) turgid, smooth and glossy. Cross section nearly circular with rounded tip. Testis creamy-white. Follicles densely packed. Alimentary canal not visible.



a) *Pecten maximus*

b) *Aequipecten opercularis*

Fig. 1.3. Gonad stages in a) *Pecten maximus* (following Mason, 1958a) and b) *Aequipecten opercularis* (following Soemodihardjo, 1974).

From the monthly sample, approximately 100 *A. opercularis* and *P. maximus* were taken and their gonad condition was observed. Only animals possessing three or more annual rings on the shell were used to ensure that, for both species, only breeding adults were selected.

The second and third methods were objective and involved weighing the gonad and other soft tissues using procedures similar to those used by Dredge (1981), Robinson *et al* (1981), Soemodihardjo (1974), Taylor & Venn (1979), Barber & Blake (1981) and Sandet & Vahl (1981). Animals of a restricted size range of 65-70 mm shell length for *A. opercularis* and 120-130 mm shell length for *P. maximus* were selected for this study (these length groups were common in the two areas). From each monthly sample 25 - 30 animals of these length groups were measured, aged and the gonad subjectively staged. The soft tissues were removed and dissected into four components, namely adductor muscle (phasic and tonic portions), gonad, mantle tissue (mantle tissue and gill) and digestive gland. These were then weighed separately to obtain fresh weights. Each tissue component was then placed in a separate pre-weighed aluminium container and dried at 60 °C to constant weight and a dry weight was measured.

The individual dry gonadal index was calculated as follows and then mean values and 95% confidence intervals were calculated for the sample (after, Sastry & Blake, 1971; Barber & Blake, 1981).

$$\text{Dry gonadal index} = \frac{\text{Dry weight of gonad}}{\text{Total tissue dry weight}} \times 100$$

1.3 RESULTS

1.3.1 The spawning cycle of *Aequipecten opercularis*

1.3.1.1 Staging method (Gross observation)

The stages of gonad development for samples of *Aequipecten opercularis* from the two grounds were determined by the subjective staging method during the period of two years extending from May 1991 to April 1993. This makes it possible to determine when spawning has taken place.

Fig. 1.4 shows the percentage frequency of spent, recovering, filling, half -full and full stages of gonad development in the monthly samples from the inshore site, Laxey Bay. The following account concentrates on the occurrence of the full and spent stages since these indicate the spawning cycle more clearly but the occurrence of other stages indicates the speed with which recovery takes place after spawning.

The frequency data show that between 29 May and 12 July 1991 there was an increase of spent gonads from 10% to 44% and a decrease of full gonads from 51% to 32%, suggesting that spawning had occurred between these dates. A rapid recovery was observed in July and August with 60% of the sampled animals in the full gonad condition by 7th August. Spawning resumed between 7 August and 29 September, with 95% of animals in the spent condition by the second week of October indicating that the major spawning period had been completed. Further evidence of this was that no more individuals with full gonads were found in this sample. The percentage of spent gonads decreased during the winter, while recovering

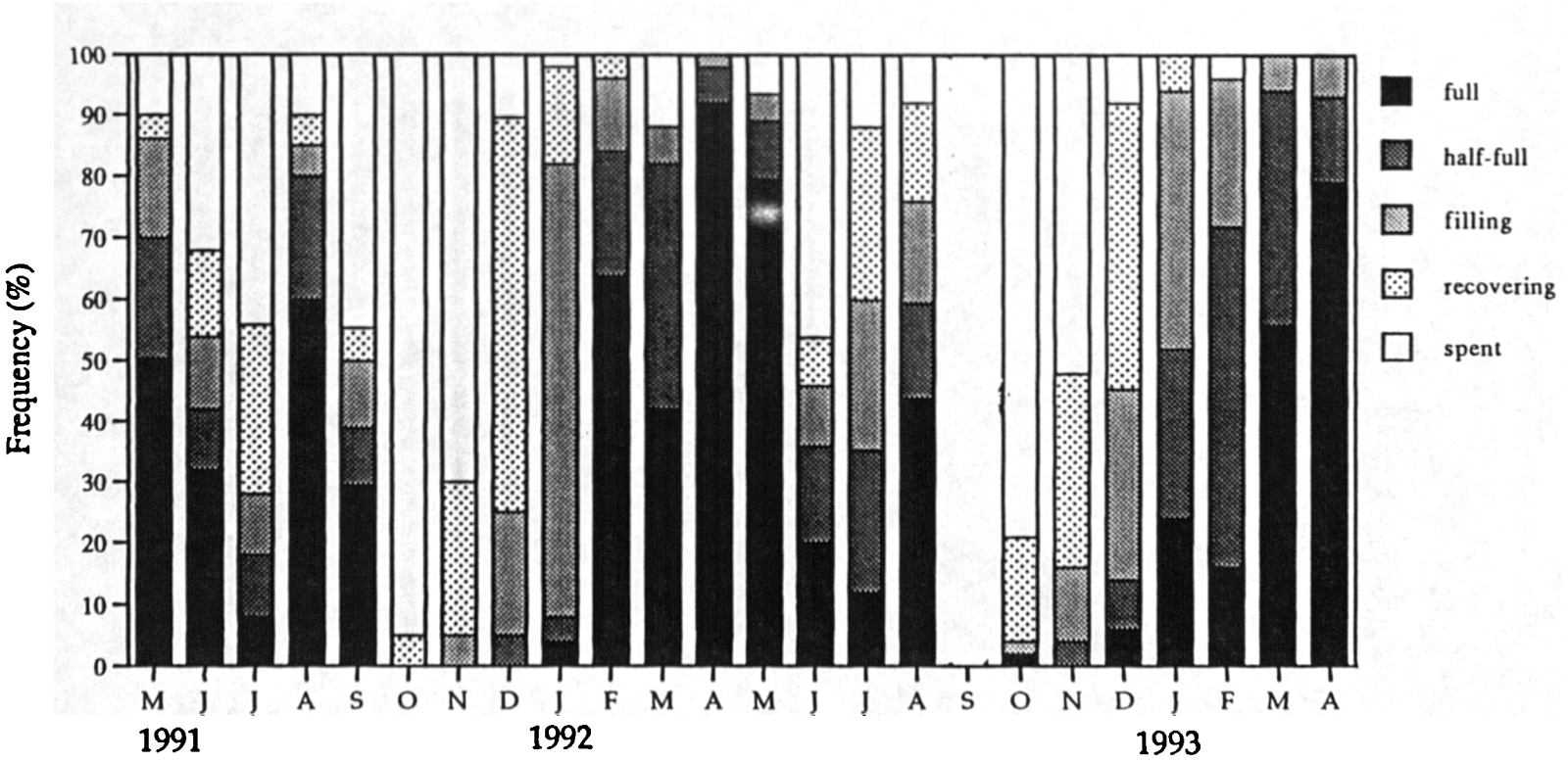


Fig. 1.4. Seasonal variations of percentage frequency of occurrence of gonads in different stages of development for *Aequipecten opercularis* (65-70 mm shell length) from Laxey Bay (no data available for September 1992).

and filling stages increased. The next sampling in the 2nd week of January 1992 showed 74% were in the filling stage.

A partial spawning was then recorded between 15 February and 25 March, with 12% spent gonads present in the March sample. The percentage frequency of full gonads increased rapidly to 92% by the last week of April. A major spawning period occurred in early summer between 18 May and 18 June when 46% of the animals were observed to be in the spent condition. A rapid recovery was recorded in July and the percentage of full gonads reached 44% in the sample taken on 10 August. Unfortunately no samples was taken in September 1992 and when sampling resumed on 16 October over 80% of the gonads were in the spent condition which suggests that the autumn spawning was completed in this period. Gametogenesis then followed through autumn and winter 1992 on a similar pattern to the previous year. In 1993 the first sample was taken in the last week of January, and contained a range of gonad stages but no spents were present. A partial spawning was then recorded between 27 January and 21 February 1993 with 4% spent gonads present in the individuals sampled on 21 February. However, recovery was rapid, and the 16 April sample consisted of 7% filling, 14% half-full and 79% full respectively. The spent and recovering stages were not present in this sample.

The general trend and pattern of spawning on the Port St. Mary offshore ground (Fig. 1.5) was similar to Laxey Bay but there were some differences shown especially during the autumn and in the period of partial spawning. The sequence starts with the 29 May 1991 sample which was composed of 33% spent, 7% recovering, 6% filling, 20% half-full and 33% full. The presence of such a high proportion of spent gonads suggests that a substantial spawning had already started in the area. This process

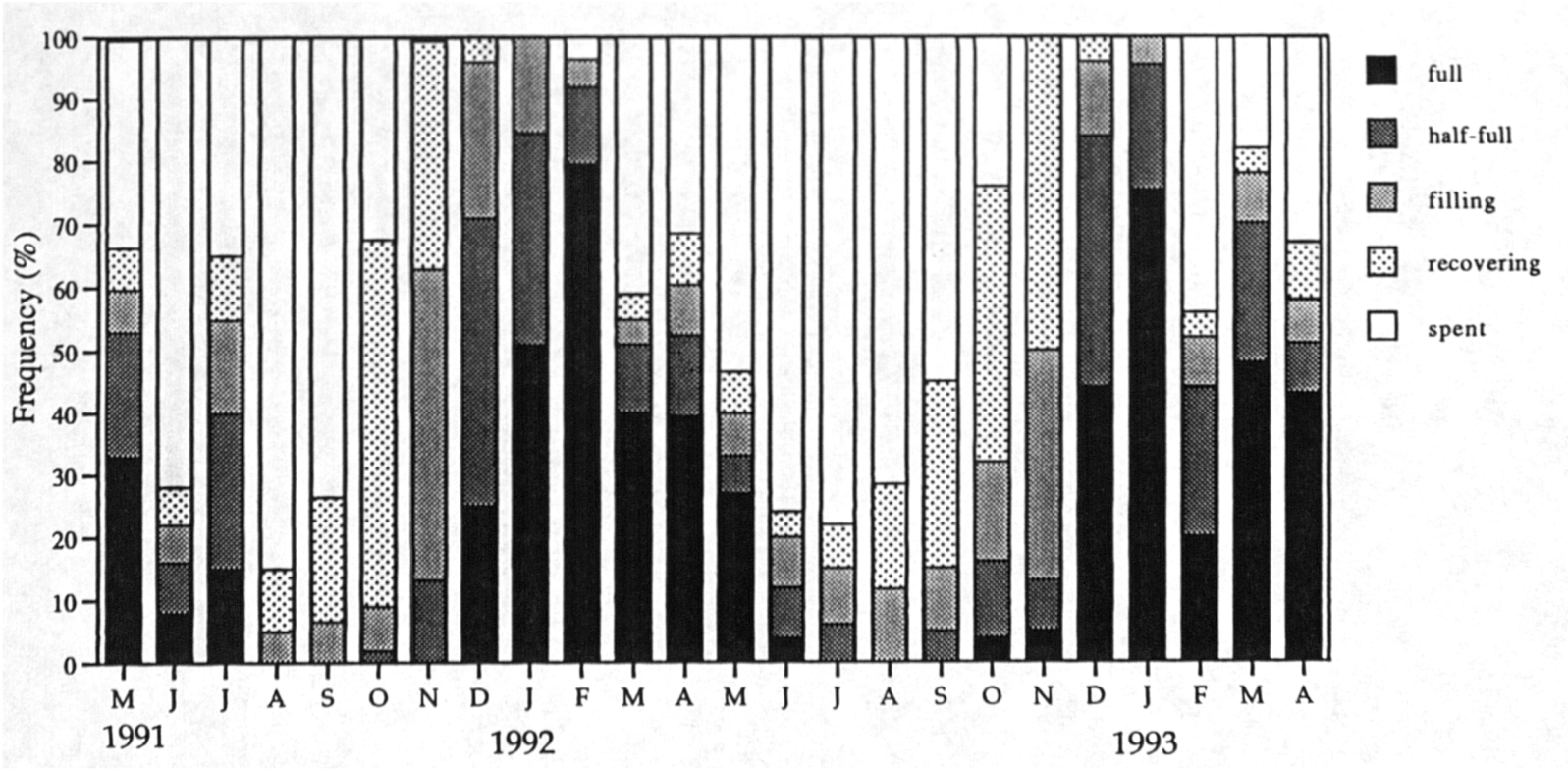


Fig. 1.5. Seasonal variation of percentage frequency of occurrence of gonads in different stages of development for *Aequipecten opercularis* (65-70 mm shell length) from the Port St. Mary ground.

continued until 21 June when 72% of the sampled individuals were in the spent condition. This early summer spawning therefore involved a rather higher proportion of the population on the Port. St. Mary ground than the samples taken from Laxey Bay in the same period. There was a small recovery in July but by 7 August 85% of the animals were again in the spent condition and no individuals were found with full gonads, indicating that spawning was over for the season. With such a high proportion of the population with spent gonads in early August and no potential spawners (full or half-full) present in the sample there was no evidence of an autumn spawning on this ground.

The recovery of the gonads started in September and development continued throughout the winter, with full gonads appearing again in the December sample. The proportion with full gonads then increased through January (51% full) to reach 79% in mid February. There was a large increase in spent gonads in the last week of March (41%) suggesting that spawning had occurred. However, a small recovery was observed by 21 April but spent gonads still made up 31% in the sample. The next sampling occurred on 18 May and spent gonad had increased to 54%, indicating that spawning had continued. By June only 4% of the individuals were in the full stage and 76% were spent suggesting that the major spawning period was over for the season. The proportion of spents increased to 78% in July and no full gonads were present. The proportion of spents then decreased steadily each month as the gonads recovered and a small proportion of full gonads appeared again in October. The pattern of recovery of the gonads was very similar to the previous year but it showed rather earlier development of the gonads compared with 1991.

By January 1993 the percentage frequency of full gonads had increased to 76% with no individuals in the spent or recovering stages. A substantial partial spawning of the population then occurred between 27 January and 21 February, by which time 44% were spent and and only 20% had full gonads. Recovery was very rapid in March when 48% and 18% of the animals were in the full and spent stages respectively. Spawning then increased and by the middle of April the proportion of spents had increased to 33% and full gonads had decreased slightly to 43%. The partial spawning in January-February 1993 was not observed in 1992.

The seasonal spawning cycles described above are illustrated more clearly in Fig. 1.6 which plots the percentage occurrence of full and spent gonads for the Laxey Bay and Port St. Mary grounds respectively.

In both years and on both grounds these two stages show very clear inverse relationships. For Laxey Bay (Fig. 1.6a) there is evidence of 3 peaks of spawning for both years. The proportion of spents shows a small peak in February or March, a moderate peak in July and a large peak in October, suggesting three spawnings of increasing intensity through the year. These peaks correspond with rapid falls in the proportion of full gonads but these are particularly sharp following the early summer spawning, suggesting that the second spawning may be of greater importance than the third.

The results for the Port St. Mary ground (Fig. 1.6b) show a similar inverse fluctuation of full and spent gonad stages but spawning peaks were less well-defined on this ground throughout the study period. Compared with the Laxey Bay population, the queen scallop population from the offshore Port St. Mary ground showed the biggest proportion of both full gonads and spents at least two months earlier in the year.

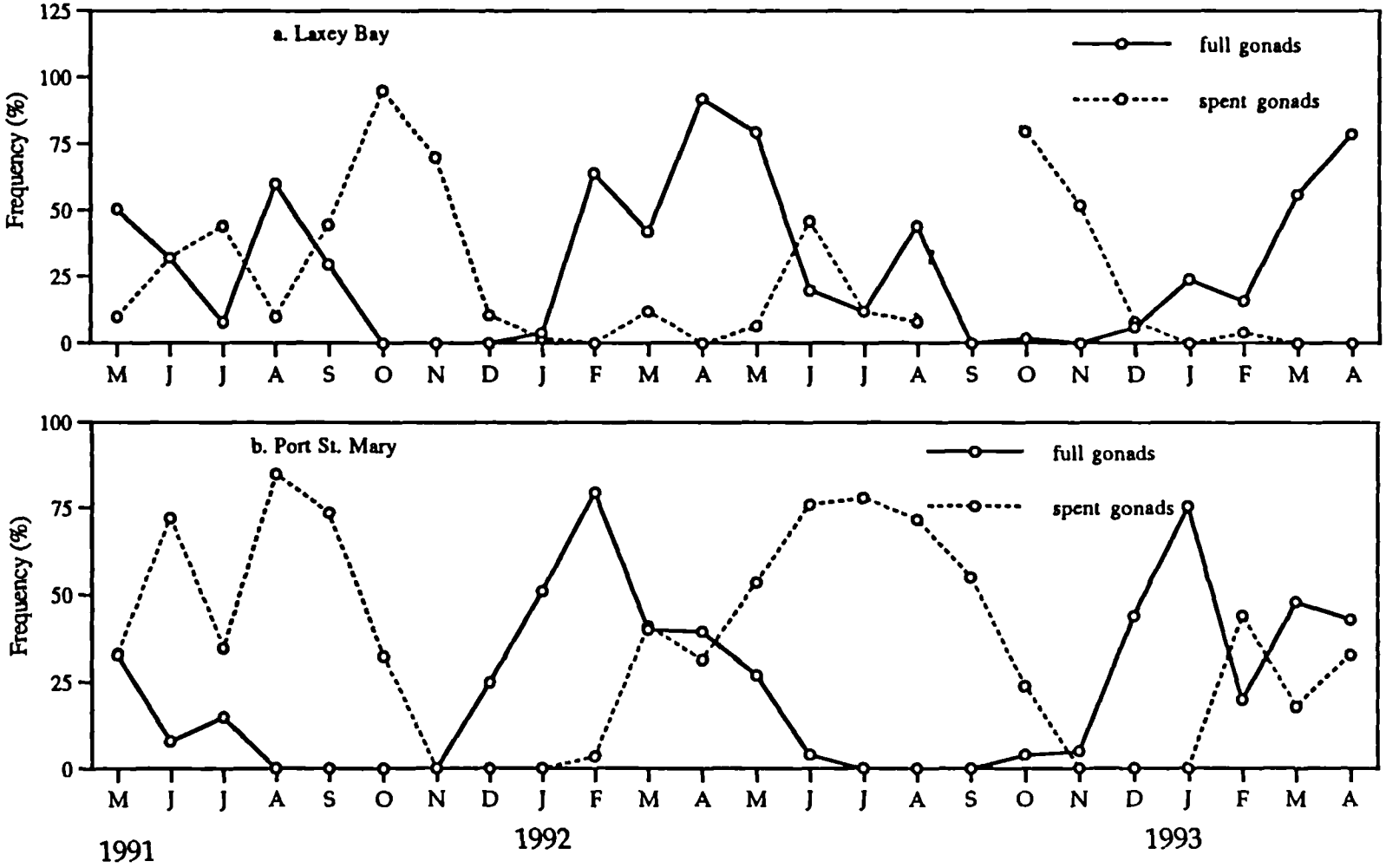


Fig. 1.6. Seasonal variation in the percentage frequency of occurrence of the full and spent gonad stages for *Aequipecten opercularis* (65-70 mm shell length) from Laxey Bay (a) and Port St. Mary (b) (no data available for September 1992 for Laxey Bay).

1.3.1.2 Gonadal index

It is clear that when the gonad is filling with reproductive tissue the gonadal index will increase and after spawning occurs the index will decrease to a lower level. Fig. 1. 7 shows the seasonal variation of gonadal index over the period of two years for the Laxey Bay and Port St. Mary populations. At the start of the period of study the gonadal index of the Laxey Bay inshore population gradually decreased from 16% to 8% between 29 May and 12 July 1991 indicating that spawning had been occurring during this period. The index recovered to 17% by 7 August, then decreased through September to reach its lowest level of 3% on 13 October indicating that a large autumn spawning had occurred. The index then remained at a low level through November and December but started to increase in January, then more rapidly to reach 18% by 15 February 1992. There was an indication of a slight fall in March but it then increased further to reach the highest level of 23% on 21 April. The gonadal index then decreased again and by 18 July it was down to only 9%, indicating that summer spawning had occurred. However, the major decrease occurred between 21 April and 18 June.

A small recovery was observed between 18 July and 10 August, the index rising to 12%. No sample was taken in September but when sampling resumed in October the index had fallen again to its lowest level of the year, indicating that further spawning had taken place in the autumn period. The index showed an increase in December and more rapidly in January to reach 21% by 16 April 1993.

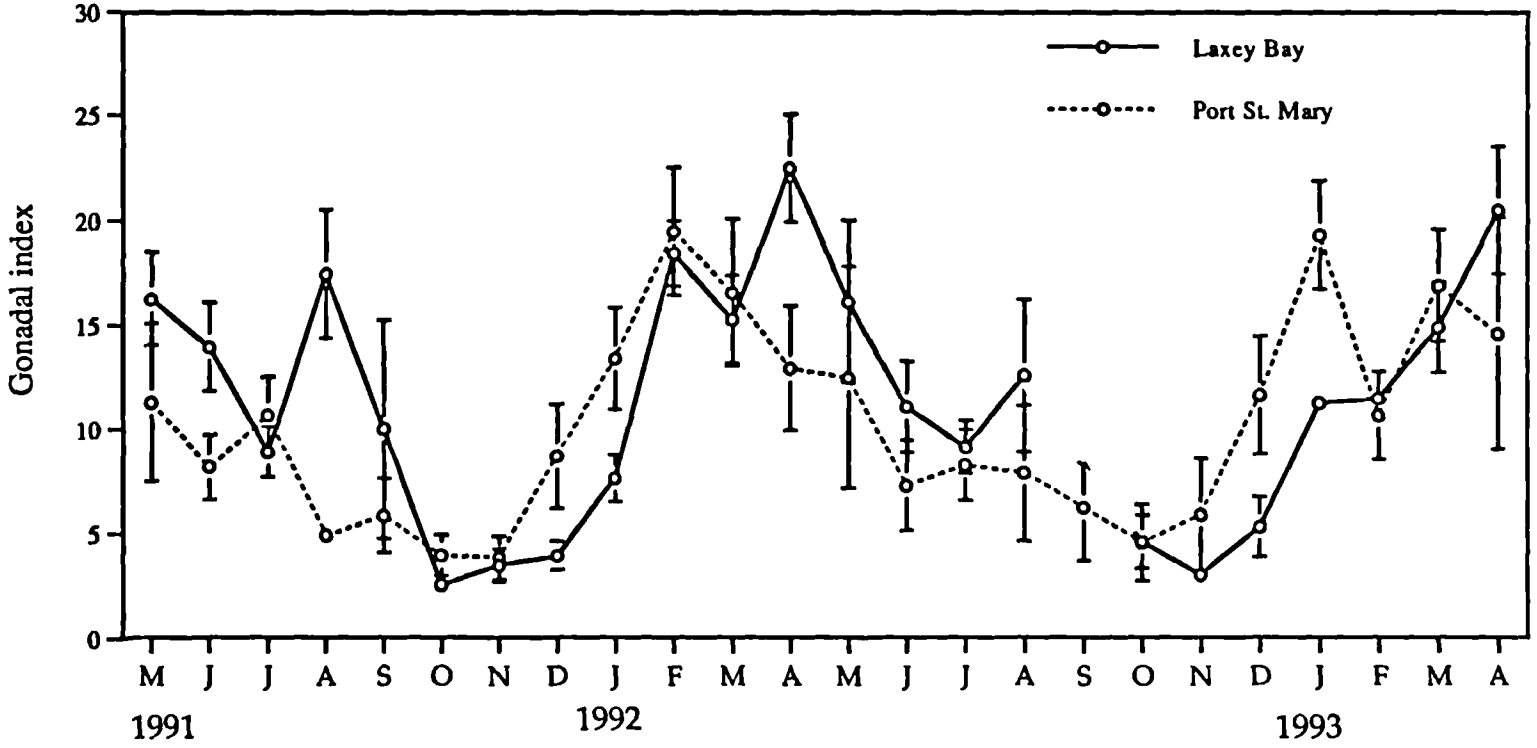


Fig. 1.7. Seasonal variation in the gonadal index of *Aequipecten opercularis* (65-70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means with 95% confidence limits. Error bars smaller than the data points do not appear on the graph (no data available for September 1992 for Laxey Bay).

The seasonal variation of gonadal index for the population on the offshore Port St. Mary ground (Fig. 1.7) followed the same general pattern as the Laxey Bay samples but there were some differences in both the level of the index and in the timing of changes. When the sampling commenced in May 1991 the gonadal index was 11% which declined to 8% by 21 June suggesting that some spawning was taking place. A short recovery was observed in July (11%) but the index then decreased to 5% by 8 August and stayed at a low level through September, October and November. No peak of spawning was therefore observed during the autumn. The index started to increase between 26 November and 11 December, then increased rapidly each month to reach 20% by 15 February 1992. It then declined steadily through spring to reach 7% by mid-June, which suggests that most of the spawning products had been released to the environment during this period. The index then remained at a low level throughout the late summer and autumn, until it started to increase rapidly between 15 November and 9 December to reach 19% by 27 January 1993. There was then a partial spawning between 27 January and 21 February indicated by the sharp fall in index to 11% but the index then rose to 17% and 15% in March and April respectively.

The gonadal indices at both Laxey Bay and Port St. Mary grounds therefore show clear annual cycles, the gonads building-up rapidly in late autumn and early winter to a high level, then falling through the spring and summer. For the inshore Laxey Bay population there appear to be three, more or less clear peaks superimposed on this general trend each year, indicating peaks of spawning in early spring, summer and autumn. For the offshore Port St. Mary population the annual fluctuations of gonadal index are smoother suggesting that spawning occurs more continuously throughout the spring and summer. During the late autumn and early

winter, when the gonadal index was increasing, the index for the Port St. Mary offshore ground was significantly higher than that for the inshore Laxey Bay, as indicated by the non-overlapping 95% confidence limits in Fig. 1.7. For the period when the index was generally decreasing through spring, summer and early autumn the index was generally significantly higher on the inshore Laxey Bay ground. These statistically significant differences result, not so much from a difference in the absolute levels to which the index rises on the two grounds, but from differences in the timing of the annual fluctuations. The annual cycle of build-up and decline of the gonadal index appears to occur one to two months earlier on the offshore Port St. Mary ground.

1.3.1.3 Gonad dry weight

Fig. 1.8 shows the seasonal variation of gonad dry weight of *A. opercularis* from the Laxey Bay and Port St. Mary grounds over the period of two years. It is very clear that the pattern of changes in gonad dry weight variation is very similar to that of the gonad index throughout the period. For the Laxey Bay inshore population, rapid decreases in mean gonad dry weight indicate peaks of spawning in late winter (1992, 1993), early summer (1991, 1992) and autumn (1991, 1992). The annual cycle was again smoother for the offshore Port St. Mary population with mean gonad dry weights indicating more prolonged spawning through spring and summer (1991, 1992) and a distinct peak in late winter (1993) but with no autumn spawning in either year. Although the mean gonad dry weight was rather more variable than the gonadal indices, there were statistically significant (95% confidence level) differences between the inshore and offshore populations, particularly during the period (November - January) when gonad weight was increasing rapidly. These again indicate that the annual cycle of gonad

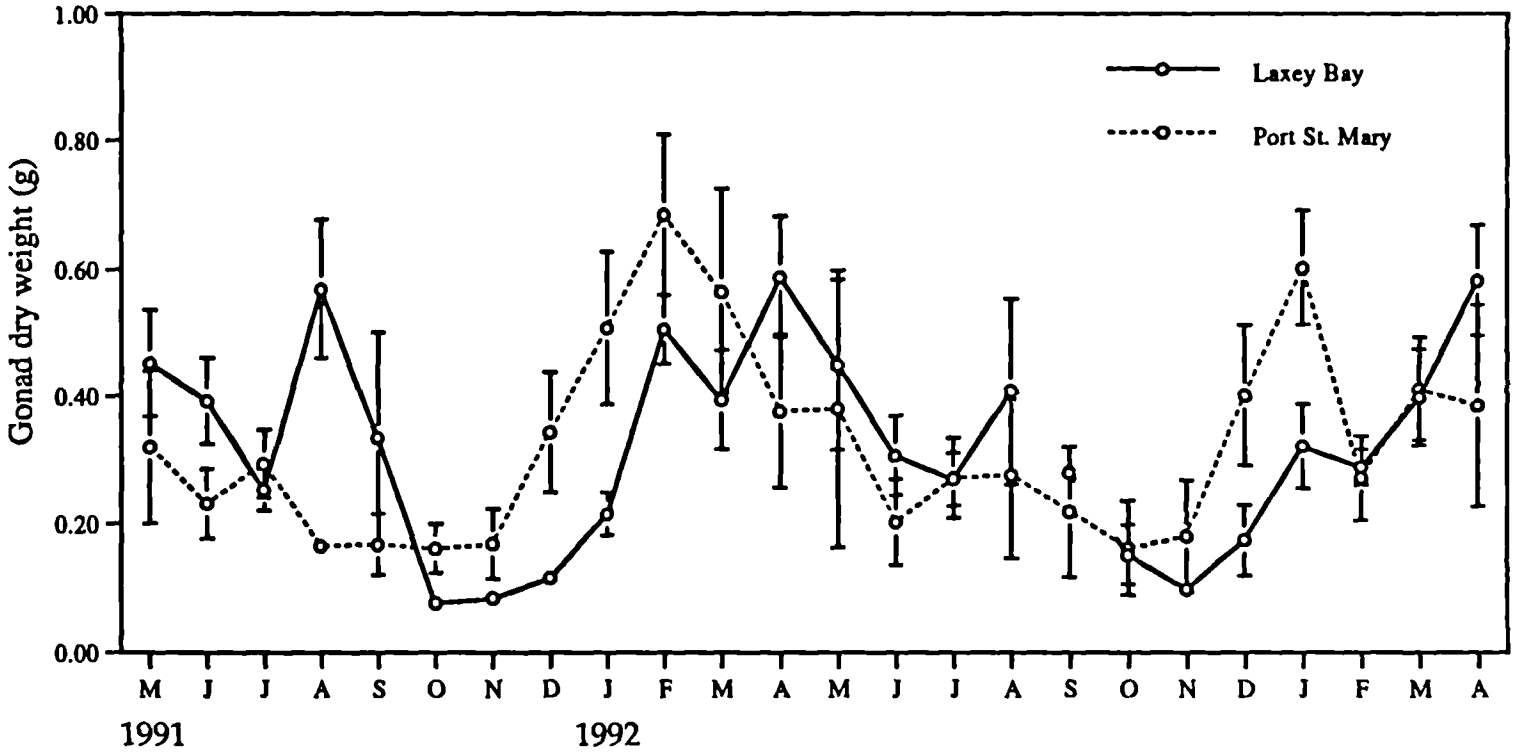


Fig. 1.8. Seasonal variation in the gonad dry weight of*Aequipectenopercularis* (65-70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means with 95% confidence intervals. Error bars smaller than the data points do not appear on the graph (no data available for September 1992 for Laxey Bay).

development and subsequent spawning generally occurred 1-2 months earlier on the offshore Port St. Mary ground.

1.3.2 The spawning cycle of *Pecten maximus*

1.3.2.1 Staging method (Gross observation)

Fig.1.9 shows the percentage frequency of individuals with spent, recovering, filling, half-full and full gonads from the inshore Laxey Bay ground. When sampling began on 29 May 1991 the percentage frequency of full and spent gonads was 53% and 10% respectively, suggesting that some spawning had recently started. The following sample collected on 21 June showed that full gonads had decreased to 7% and 58% were spent, indicating that the majority of the population had spawned. By the middle of June the few remaining individuals with full gonads had spawned and the percentage of spents had increased to 70%. At the same time there was an increase in the proportion in the recovering stage and by August 12% had full gonads. However, in the following sample, collected on 18 September, no gonads were found in the full condition suggesting that some spawning had occurred between August and September. Recovery continued throughout the autumn and early winter (October - December) with no gonads observed in a spent condition after October. By January 1992 the majority of the population were in the recovering (5%), filling (64%) or half-full (30%) stages. No gonads were observed in a spent condition. Full gonads appeared again in February, increasing rapidly to 83% by 25 March and remained in a similar state until April. A major spawning then occurred with 57% being spent on 18 May, increasing to 79% by 18 June and with no full individuals in the sample.

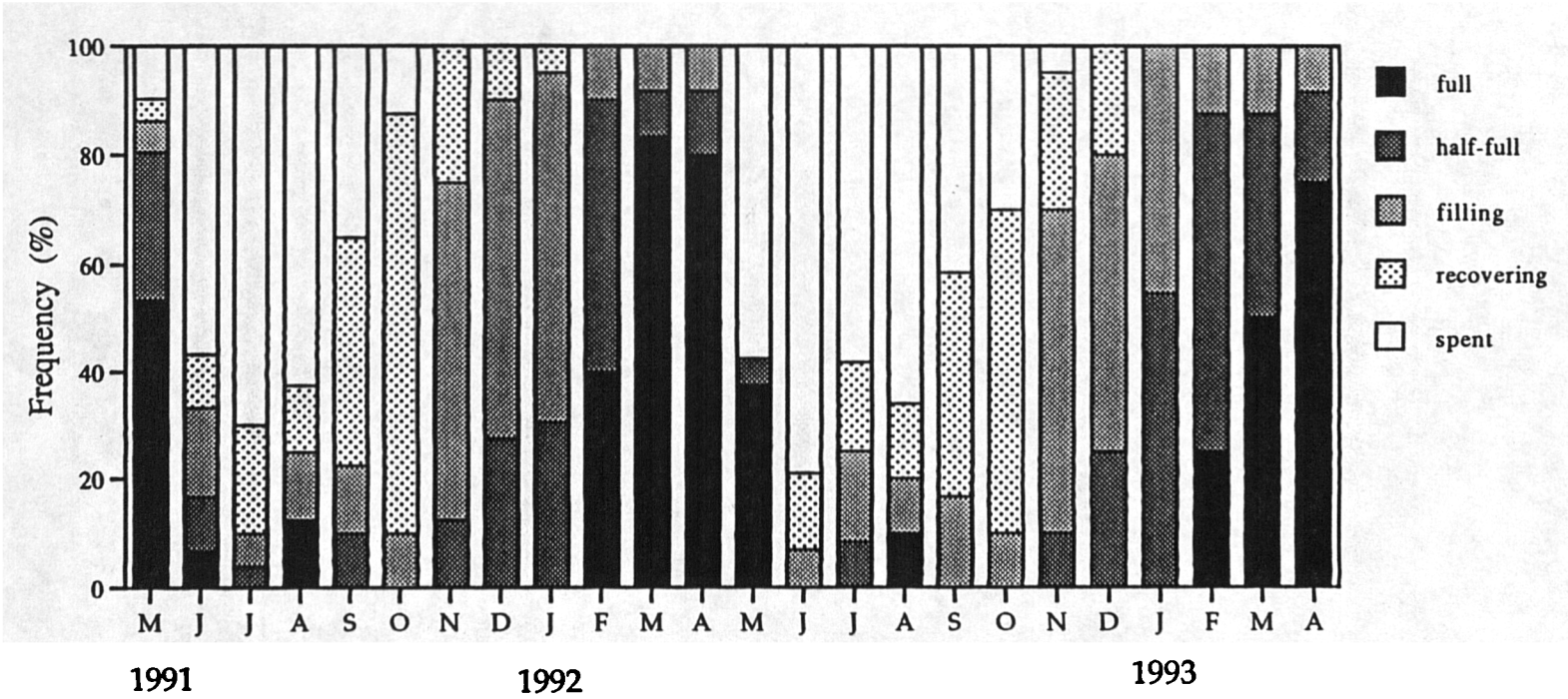


Fig. 1.9. Seasonal variations of percentage frequency of occurrence of gonads in different stages of development for *Pecten maximus* (120-130 mm shell length) from Laxey Bay.

Recovery and filling continued through July and by 10 August the percentage of full gonads in the sample had increased to 10%. These animals then spawned and no individuals were observed in the half-full or full condition in samples from the middle of September suggesting that the spawning was over for the season.

Recovery of the gonads continued over the autumn and winter, following a similar pattern to that observed in 1991/92, with full gonads reappearing in February and increasing rapidly until the 16 April 1993 sample which was composed of 16% in the half-full and 75% in the full stages.

The results for the Port St. Mary ground (Fig.1.10) showed a similar spawning pattern to Laxey Bay during 1991. Spawning had already started when sampling commenced on 29 May and the proportion with spent gonads increased rapidly to 70% by the fourth week of June. There was, however, no indication of a large autumn spawning on this ground. No full gonads were present after June and the percentage of spent gonads remained high and comparatively constant from 21 June through to 29 September. When the next sample was taken on 20 October, 20% of the individuals were still in a spent state but there was a strong indication of recovery. The percentage of spent gonads then decreased while the frequency of recovering, full, and half-full gonads increased during November and December, and by the last week of January 1992 the majority of individuals were in an advanced stage of gonad development (33% half-full, 53% full). This process continued gradually through February and March so that by the last week of April 83% of gonads were in the full state. Spents appeared in the samples taken on 18 May and 18 June but did not form a high percentage until 18 July when 70% of the animals were spent. The proportion of spent gonads remained high and fairly constant through

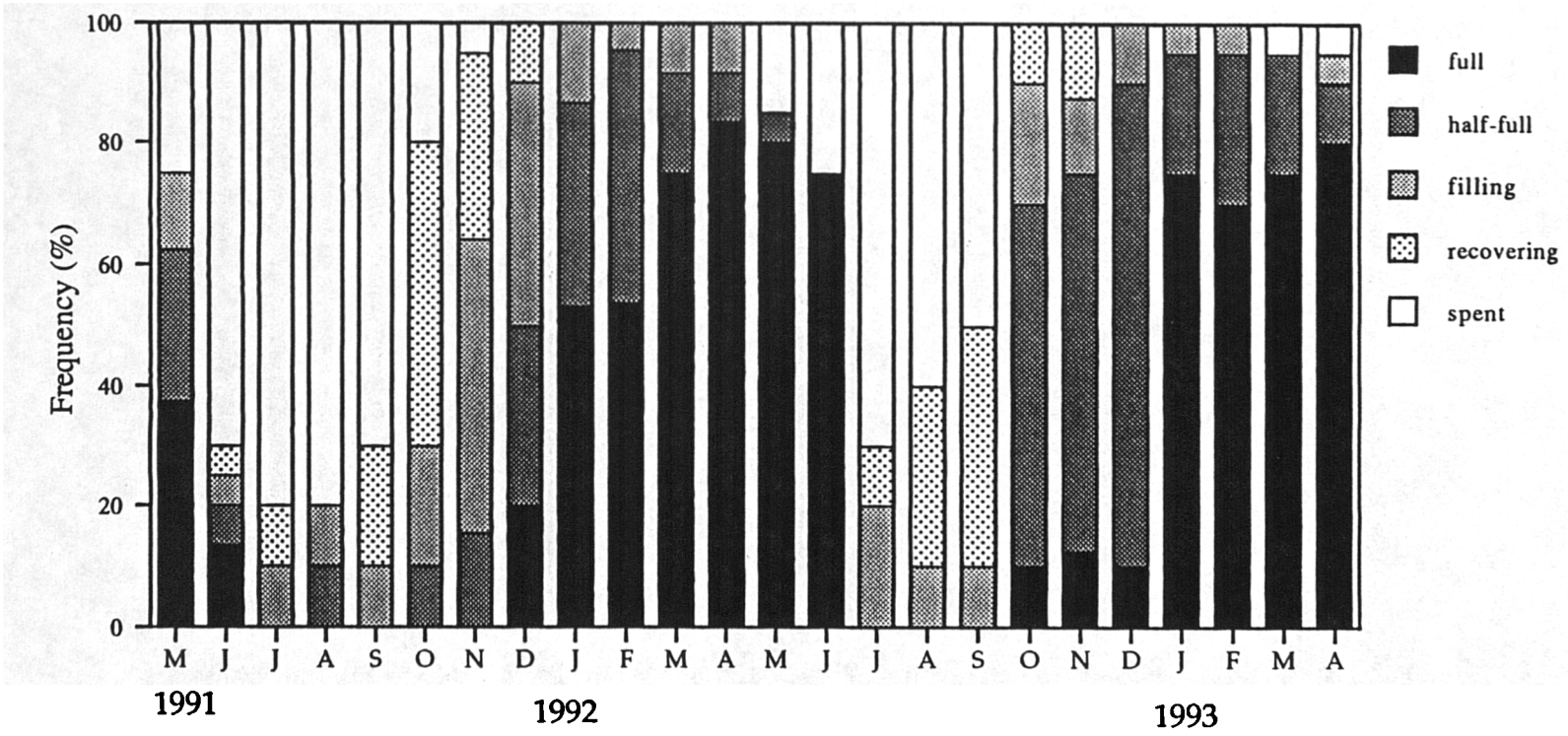


Fig. 1.10. Seasonal variations of percentage frequency of occurrence of gonads in different stages of development for *Pecten maximus* (120-130 mm shell length) from Port St. Mary.

August and September, and no full or half-full gonads were present which again indicates the absence of any late summer or autumn spawning. The recovery of the gonads then proceeded through autumn and winter with the percentage of full gonads rising rapidly between 9 December and 27 January to 75%. It then remained at this level until the end of the sampling period, though a small proportion of spents (5%) were present in the March and April samples.

The pattern of spawning on the two grounds is illustrated more clearly in Fig.1.11 which shows the changing proportions of full and spent gonad stages for the Laxey Bay and Port St. Mary grounds respectively. For both populations the main spawning appears to occur in early summer, though it was notably earlier on the inshore Laxey Bay ground in 1992. For the Laxey Bay population the small but distinct second peak in the percentage of full gonads in both 1991 and 1992, indicates that a second minor peak in spawning occurred in August- September, though this was not readily apparent from the proportion of spents. In contrast, there was no evidence of any late summer or autumn spawning for the offshore Port St. Mary population but the subsequent recovery of the gonads to the full condition through autumn and winter proceeded 1-2 months earlier than in Laxey Bay in both years.

1.3.2.2 Gonadal index

Fig. 1.12 shows the seasonal changes of gonadal index of *P. maximus* from Laxey Bay and Port St. Mary during the two year period of this study. At the beginning of the investigation in May 1991 the gonadal indices were very similar at the two grounds (24% and 21% respectively), and they decreased steadily through early summer indicating that spawning was

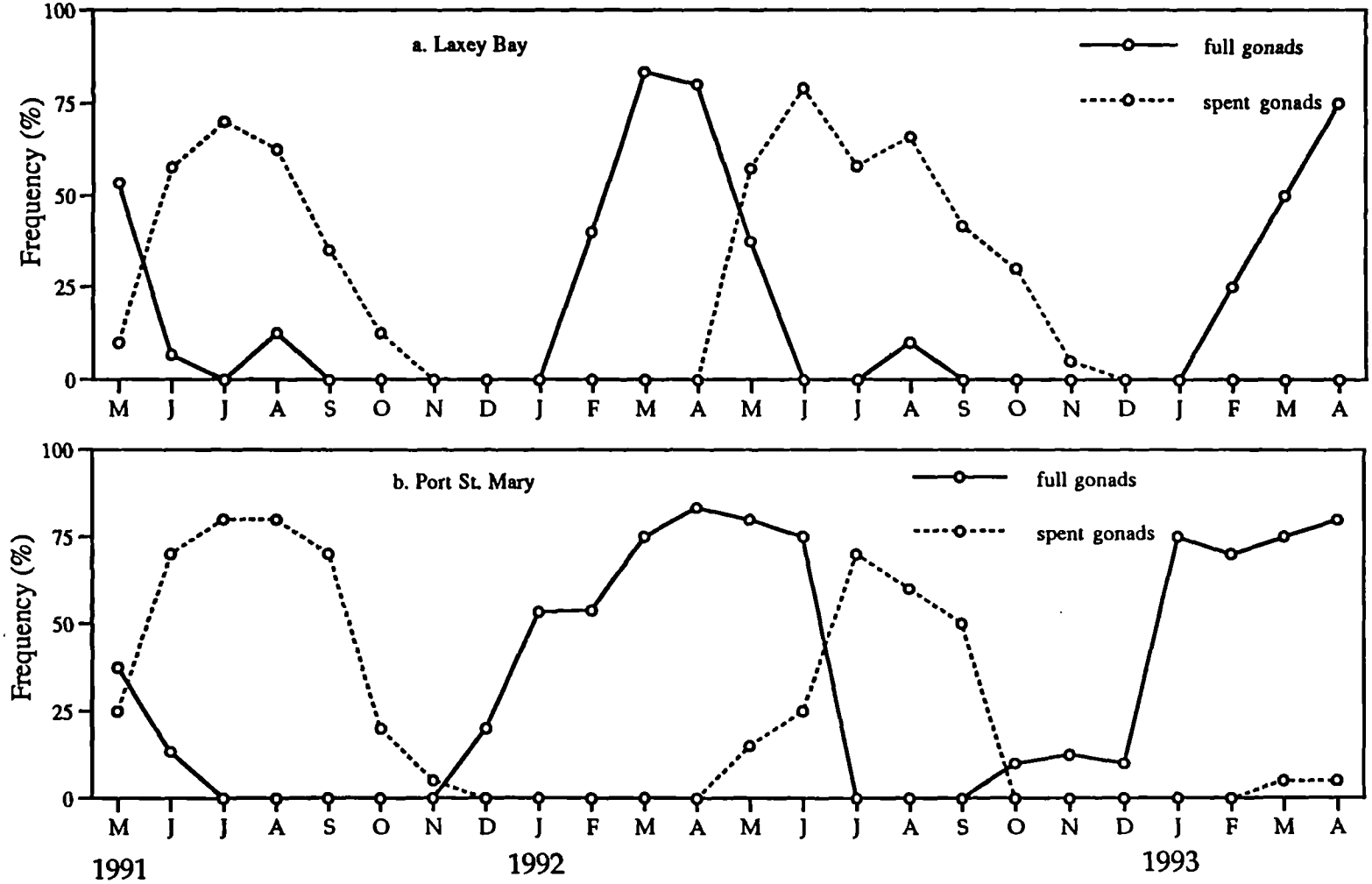


Fig. 1.11. Seasonal variation in the percentage frequency of occurrence of the full and spent gonads stages for *Pecten maximus* (120-130 mm shell length) from Laxey Bay (a) and Port St. Mary (b).

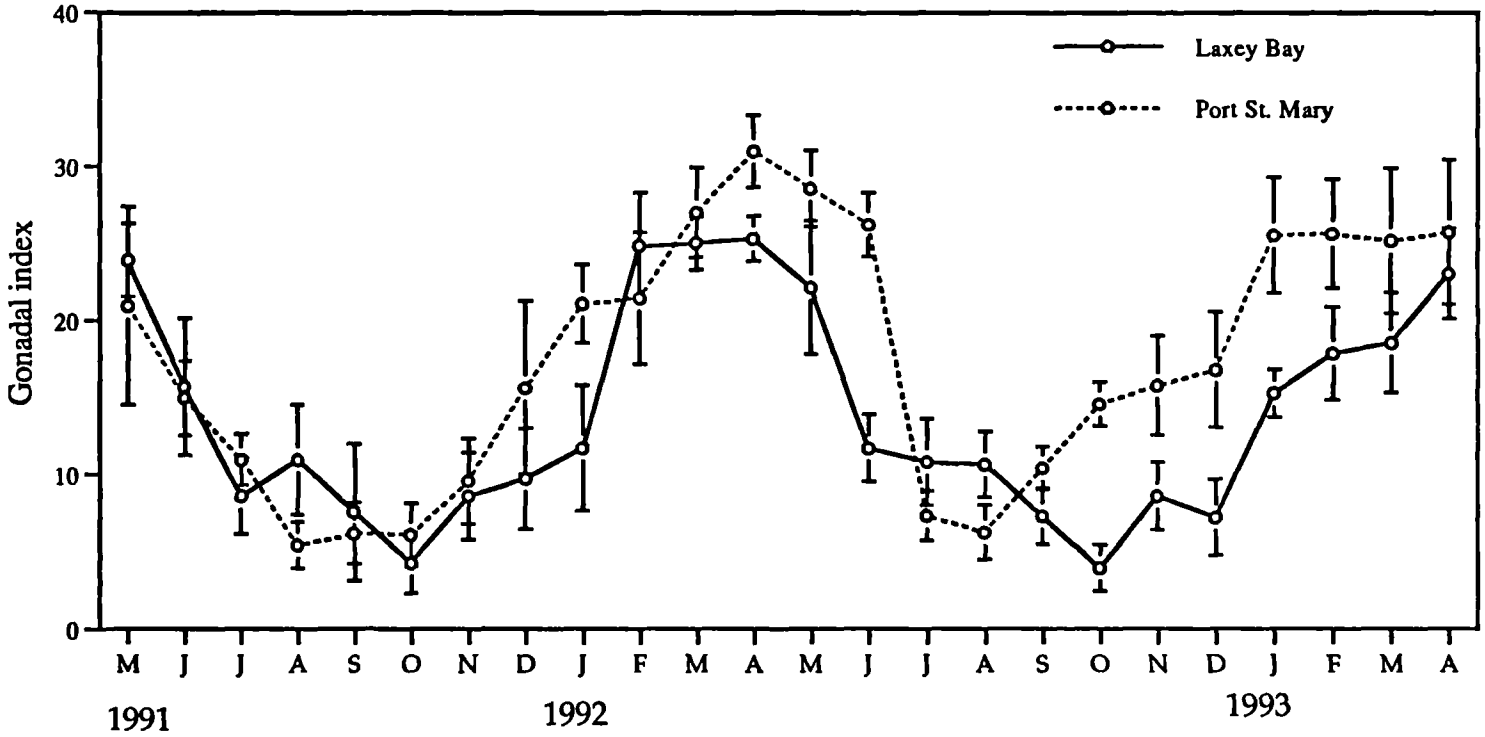


Fig. 1.12. Seasonal variation in gonadal index of *Pecten maximus* (120-130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means with 95% confidence intervals.

occurring. The index at Laxey Bay showed a 2% increase in August, while that for the Port St. Mary ground continued to decreased. In consequence, there was a statistically significant difference (95% confidence level) in the gonadal index values for the two grounds in August 1991. The index for the Laxey Bay population then decreased over the following two months, suggesting that further spawning was occurring. Recovery of the gonadal index started earlier on the offshore Port St. Mary ground, building-up through winter and early spring to reach its highest level in April 1992 (31%).

For the inshore Laxey Bay ground recovery followed a similar pattern, but the build-up started later and did not attain such a high level (23%). As a result the gonadal index values recorded for the two grounds were generally statistically different throughout the recovery period. In contrast to 1991, the sharp decline in the gonadal index indicating spawning in 1992 occurred one month later on the offshore Port St. Mary ground than at Laxey Bay. The index on this ground fell rapidly between June and July, then declined a little further to its lowest level in August but was immediately followed by a recovery in September that continued throughout the winter and early spring. For the Laxey Bay population the gonadal index fell rapidly between May and June but then levelled off and remained at about 10% for two months before falling again to its lowest level in October. As in 1991, this suggests that some late summer or autumn spawning occurred on this ground. Recovery then followed and the index continued to increase for the rest of the study, but with the recovery starting two months later, the values of the index were significantly lower than for the offshore Port St. Mary ground throughout this period. The pattern of change in gonadal index therefore differred on the two grounds, though it was generally fairly similar on each ground for the two years studied. For

most months the index was significantly higher on the offshore Port St. Mary ground, where recovery of the gonads in the autumn occurred 1 - 2 months earlier and spawning in the summer was later (in 1992 only) than on the Laxey Bay inshore ground.

1.3.2.3 Gonad dry weight

The seasonal variations in gonad dry weight of *Pecten maximus* from Laxey Bay and Port St. Mary are shown in Fig.1. 13. The weight of gonad tissue at both sites followed a similar pattern to the gonadosomatic index throughout the study period, differing only slightly. From when sampling started in May 1991, the mean dry weight of gonad of both populations decreased in a similar way until 12 July, when a small recovery was recorded at Laxey Bay in August, before declining again in October. The mean dry weight of gonads at Port St. Mary ground decreased until August, then started to regain weight over the autumn and winter, reaching its maximum level in April 1992. The increase in weight at Laxey Bay started later and was very slow in November and December but increased rapidly in January 1992 to its highest level in the 15 February sample. Mean dry gonad weight then started to decline at both sites. This decline was slow initially but with rapid drops between 18 May and 18 June at Laxey Bay, and between 16 June and 24 July at Port St. Mary indicating the main spawning periods. The mean gonad dry weight during the spring and early summer was significantly different at the 95% confidence level in these two populations (Fig. 1. 13). The mean dry weight at Laxey Bay remained relatively constant in June and July before dropping to a low level in October, suggesting that some autumn spawning had recently occurred.

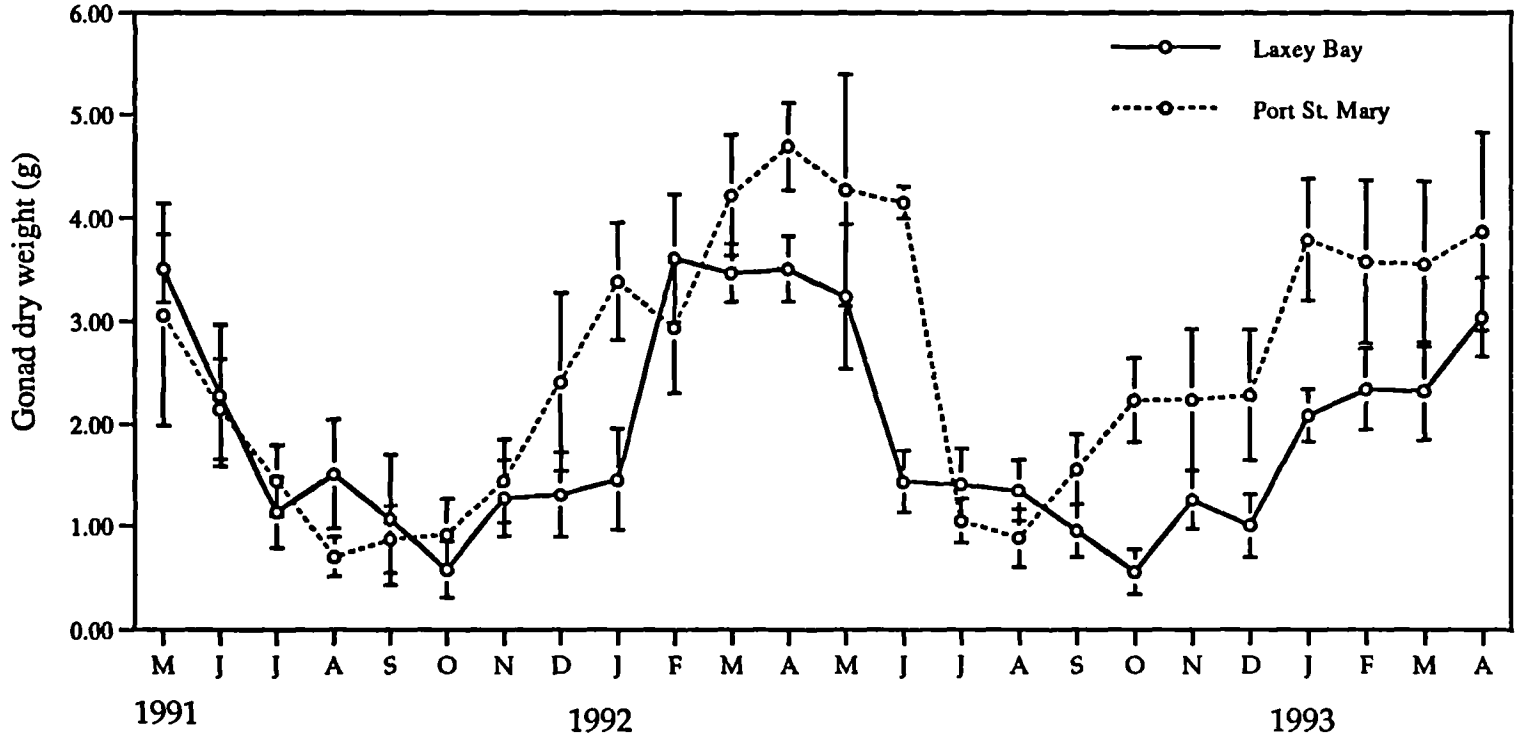


Fig. 1.13. Seasonal variation in gonad dry weight of *Pecten maximus* (120-130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means with 95% confidence intervals.

For the Port St. Mary ground there was no indication of any autumn spawning. Gonad mean dry weight increased steadily from its lowest level in August until 27 January 1993, then remained constant until the end of the study. After the autumn spawning the build-up of the gonads on the Laxey Bay ground started some two months later and continued until the last sample was taken on 16 April. Mean gonad dry weight was therefore significantly lower (95% confidence level) for the Laxey Bay population than the Port St. Mary offshore population for most months throughout 1992 and 1993.

1.4 DISCUSSION

The scallop spawning cycle, as in other molluscs, is a genetically regulated response to the environment (Sastry, 1970a, b, Sastry and Blake, 1971; Blake & Sastry, 1979). The nature of the gametogenic cycle in a species is determined through the co-ordination of reproductive events with changes in exogenous features, such as food, temperature, light, salinity and tides, and endogenous control by nervous and hormonal systems within an organism (Sastry, 1979). The timing, duration and number of gametogenic cycles may therefore differ in populations of species occurring in different parts of the world (Broom, 1976; Sastry, 1979; Duggan, 1987; Paulet *et al.*, 1988).

Most scallops from temperate and warm seas spawn at an age of slightly less than one year (Belding, 1910; Gustell, 1931; Aravindakshan, 1955; Mason, 1957; Reddiah, 1962; Broom, 1976; Dredge, 1981). However, the scallop *Pecten maximus*, in Manx waters, first spawns in the autumn following the deposition of the second growth ring, when most are about two years old (Mason, 1957). The queen, *Aequipecten opercularis* reaches maturity and spawns for the first time when 1-2 years old (Aravindakshan, 1955). The size groups selected for this study ensured that all the animals studied were past the age of first maturity.

In this study three methods (staging, gonadal index, gonad dry weight) were used to determine spawning cycles of both species. Each method has limitations and there are different implications in their use. One general problem, common to all three methods, was the long interval of 3 - 4 weeks between samples. Major spawnings may occur in a day when environmental conditions are suitable (Aravindakshan, 1955; Paul,

1978), so the long interval between samples inevitably restricted the precision with which spawning events could be determined. Ideally, for such a study, samples should be taken at weekly intervals, or even more frequently around the time of spawning. Unfortunately, in this study, such frequent sampling was not logistically possible. The staging method in particular may not detect minor spawning activities which take place during the observation period. A further difficulty is that spent gonads are often prominent for long periods without recovery and this can lead to misinterpretation of the spawning peak in a particular period. This situation was clearly observed in both *A. opercularis* and *P. maximus* from the Port St. Mary ground. After the summer spawning (May/June) the spent gonads of these populations were retained until sometime in November. Reduced sampling intervals, together with stereological observations have enabled this method to be used to give clear assessments (Barber & Blake, 1981; Sundet and Lee, 1984; Mackie, 1986; Beninger, 1987; Lubet *et al.*, 1987a; MacDonald & Bourne, 1987).

The weight analysis methods (gonadal index and gonad dry weight) probably better describe the duration of spawning periods of pectinids (Ito *et al.*, 1975; Bergeron & Buestel, 1978; Latroit, 1978; Duggan, 1987). This is true for both *A. opercularis* and *P. maximus* in Manx waters. The gonad of scallops separates easily from the other tissues, compared with other bivalve species, making these methods particularly appropriate. As the gonad matures, it increases in weight and size. After spawning and the release of gametes the gonads become smaller and decrease in weight. The weight of adductor muscle and digestive gland are inversely related to the gonad weight. These changes in the tissues can easily be used to predict spawning cycles. The gonadal index provides a comparative estimate for animals of different sizes but increases or decreases in the

index can result from variations in other tissues and do not necessarily indicate changes in gonad size or output. Gonad dry weight provides the best assessment of reproductive output but this method always requires the use of restricted length groups or calculation for a 'standard animal' (Comely, 1974; Ansell, 1974a, b, c; Soemodihardjo, 1974). Using all these methods simultaneously undoubtedly aided the intrepretation of events in the present study.

1.4.1 Spawning cycle of *Aequipecten opercularis*

The spawning cycle of *A. opercularis* has been shown to vary between different locations (Broom, 1976; Paul, 1978) and some peak spawning periods recorded throughout the geographical range are summarised in Table 1.3. At the northern end of the geographical range Ursin (1956) noted some minor differences in timing of the main spawning between Danish waters (July - August), the North Sea (August - September) and Faroe waters (July - August). Fullarton (1889) observed one peak spawning period of *A. opercularis* in the Firth of Forth during August - September, whereas Dakin (1909), in the same area, noted the peak spawning to be slightly earlier in July - August.

In the Clyde Sea area of the west coast of Scotland, Taylor & Venn (1979) reported two peaks of spawning, a summer spawning in June-July and an autumn peak in September- October. Richardson (1983), however, noted only a single rather earlier (March-June) peak in the same area.

In the Irish Sea there have been a series of investigations in the waters around the Isle of Man. Aravindakshan (1955) observed three peaks of spawning a year for *Aequipecten opercularis* off the south end of the Isle

Table 1. 3. Peak spawning periods of *Aequipecten opercularis* recorded in some different regions, throughout the geographical range.

Location	Spawning period	Method of assessing	Source
Faroe waters	July - Sep.	SM	Ursin (1956)
Danish waters	July - Aug.	SM	Ursin (1956)
North Sea	Aug. - Sep.	SM	Ursin (1956)
Firth of Forth, UK	Aug. - Sep.	SM, L, S	Fullarton (1889)
Firth of Forth, UK	July - Aug.	SM	Dakin (1909)
Clyde Sea, UK	June - July		
	Sep. - Oct.	SM, GW	Taylor & Venn (1979)
Clyde Sea, UK	Mar. - Jun.	SM, S	Richardson (1983)
Isle of Man	Jan., June, Aug., Sep.	SM	Aravindakshan (1955)
Isle of Man	June - July Sep. - Oct.	SM, GW	Soemodihardjo (1974)
Isle of Man	June - July	S	Brand (1976)
Isle of Man	Feb.		
	June-July		
	Sep. - Oct.	SM, GW, S	Paul (1978)
Isle of Man	June - July		
	Sep. - Oct.	S	Brand *et al.* (1980)
Isle of Man	Mar.- Apr.		
	June - July	SM, GI, S	
	Sep. - Oct.		Duggan (1987)
Isle of Man	June -Aug.	SM	Allison (1993)
Isle of Man (Laxey Bay)	Feb. - Mar.		
	June - July		
	Aug. - Sep.	SM, GI, GW	present study
Isle of Man (Port St. Mary)	Feb. - Mar.	SM, GI, GW	present study
	May - June		
Langstone harbour, Hampshire, UK	Jan. - Feb.		
	June - July		
	Sep. - Oct.	SM	Broom & Mason (1978)
Plymouth, UK	Jan. - June	SM	
	Aug.		Amirthalingam (1928)
Venezia, Italy	June, Sep.	S	Renzoni (1991)

SM (staging method), GW (gonad weight), GI (gonadal index), L (larval abundance) and S (spat abundance).

of Man, which fell in January, June and August or September. However, Soemodiharjo (1974) observed only two spawning peaks for queens from the Port Erin ground, the first occurring during June - July and the second during September - October. Paul (1978) collected samples from south of the Isle of Man on the Chicken Rock and Bradda Head grounds and observed three periods of spawning. The first occurred in February followed by a recovery, leading to a summer spawning period during June - July. An autumn spawning was noted in September and October. Duggan (1987), using the same grounds, observed the first breeding in March - April, followed by a summer spawning in June - July and an autumn spawning in September - October.

The spawning pattern of *A. opercularis* observed in the present study resembled the observation made by Aravindakshan (1955), Paul (1978) and Duggan (1987) for the Laxey Bay population but the offshore Port St. Mary population was rather different in that only two spawning peaks were apparent. A partial spawning occurred in both populations between February and March in both years. Aravindakshan (1955) and Paul (1978) also observed this in February, while Duggan (1987) noted it later, in March-April. Soemodihardjo (1974) and Duggan (1987) considered partial spawning to be at a low intensity but the 'minor' spawning on the Port St. Mary ground showed a relatively high intensity in February 1993, when up to 40% of the population were in a partial spawning state. Paul (1978) noted that partial spawning can make a considerable contribution to the overall spat settlement on some occasions. Soemodihardjo (1974) considered this winter spawning to be part of the autumn spawning of the previous year. This was followed by the summer spawning peak, which in Laxey Bay was between June-July, while in Port St. Mary it occurred somewhat earlier in May-June.

On the Laxey Bay fishing ground there was then a well-pronounced autumn spawning, which from the proportion of spents in the population appeared to be quite important, particularly in 1991. In contrast, there was no evidence of an autumn spawning in the Port St. Mary population in either year of the study. Instead, the spawning peaks were less well-defined and the redevelopment of the gonads through the autumn and winter proceeded some two months earlier than for the Laxey Bay population.

Considering the results obtained by the three methods of assessment (staging, gonadal index, gonad weight) together it is apparent that the greatest weight gain or the presence of a higher percentage of full gonads occurred before the summer spawning, and the greatest weight loss or severe depletion of full gonads occurred after the summer spawning. On this basis it must be concluded that for *A. opercularis,* over this two year period, the summer spawning was more important than the autumn spawning for both populations.

The summer spawning of *A. opercularis* has been observed on many occasions around the Isle of Man (Aravindakshan, 1955; Soemodihardjo, 1974; Paul, 1978; Duggan, 1987) and in other European waters (Broom & Mason, 1978; Taylor & Venn, 1979). Observations of spat settlement of *A. opercularis* around the Isle of Man showed that the summer spawning was most productive for spat settlement on collectors (Brand, 1976; Paul, 1978; Brand *et al.*, 1980; Duggan, 1987). Whittington (1993) considered the larval life variation to be of between 3-6 weeks and collected more spat on artificial collectors in early autumn, concluding that these were derived from the summer spawning. Ventilla (1977) collected spat of *A.*

opercularis in Ardnamurchan Bay off the west coast of Scotland and observed peak settlement in late July. Similar summer peaks of spat settlement were also observed by McKay (1976) in sea lochs around the Isle of Mull and by Fegan (1983) in the Oban area in Scotland.

Although the summer spawning was more intensive for both populations, the autumn spawning, which occurred in Laxey Bay in both 1991 and 1992, also represented a considerable contribution. Aravindakshan (1955), Soemodihardjo (1974) and Paul (1978) indicated that, in certain years, the autumn spawning appeared to be more intensive than the summer spawning. Duggan (1987) provided results for spat collection during 1983 which showed that the autumn spawning resulted in the greatest spat fall, although spat were also collected in reasonable numbers following the summer spawning.

The use of spat collection studies to investigate regional differences in spawning cycles is, of course, problematic since the origin of settling (and surviving) spat is difficult to establish. Some relevant information in this regard has come from recent genetic studies of Irish Sea queens. Macleod *et al.* (1985), like Beaumont (1982a), considered that Irish Sea queen stocks represented one panmictic population but a more detailed study by Lewis (1992) has shown that stocks on the east and the west side of the Isle of Man are at least partially genetically isolated. Until more direct evidence is available to link spawning with settlement and the subsequent recruitment of queenies, the relevance of small differences in the seasonal pattern of spawning over relatively small geographical distances, such as demonstrated here for the Laxey Bay and Port St. Mary fishing grounds, will remain unclear (see, general discussion).

Two or more peaks of spawning each year appears to be the normal pattern for *A. opercularis* populations further south in its geographical range (Table 1.3). Thus three main spawnings have been recorded in Langstone Harbour, Hampshire (Broom & Mason, 1978) and two in the Mediterranean (Renzoni, 1991), while at least four main spawning peaks, extending from late winter to the middle of summer, occur in the rias of Galicia, Spain (Roman, 1991). The general trend, throughout the latitudinal range, therefore appears to be for a single spawning period at the northern end of the range, and multiple peaks at the southern end but local conditions can result in different spawning patterns in some closely-located populations.

1.4.2 Spawning cycle of *Pecten maximus*

The seasonal pattern of spawning of *P. maximus*, like that of *A. opercularis*, varies in different locations (Table 1.4). As with *A. opercularis*, there are latitudinal differences in the timing and number of spawning peaks, though for *P. maximus* there are rarely more than two peaks each year. At the northern end of the range, in western Norway, Strand & Nyland (1991) recorded single spawning peaks for two populations of scallops, the most northerly having a closely-synchronised spawning in June and the more southerly a less well-synchronised spawning in late July-August or August-September. In Loch Creran, on the west coast of Scotland, there is also one main spawning period each year but timing can vary from year to year and spawning is not closely-synchronised between all individuals in the population (Fegan *et al.*, 1985; Mackie, 1986; Ansell *et al.*, 1991). Similarly, in the Clyde Sea area, there is also a single summer spawning peak (Comely, 1974).

Table 1. 4. Peak spawning periods of *Pecten maximus* recorded in some different regions, throughout the geographical range.

Location	Spawning period	Method of assessing	Source
Fosen, W. Norway	June	SM, GI, H	Strand & Nyland (1991)
Austevoll, W. Norway	July -Sep.	SM, GI, H	Strand & Nyland (1991)
Loch Creran, UK	May - Jun.	SM, GW, GI L	Fegan *et al.* (1985)
Loch Creran, UK	May - Jun.	GW, H	Mackie (1986)
Clyde Sea, UK	June - July	SM, GW	Comely (1974)
Northern Ireland	May, June Aug.	GW, GI	Stanley (1967)
Isle of Man	Apr. -Aug.	SM	Dakin (1909)
Isle of Man	Apr. - Jun.	SM, MO, L	Tang (1941)
Isle of Man	Apr. - May Aug. - Sep.	H	Mason (1958a)
Isle of Man	Apr. - May Sep. - Oct.	GW, GI	Duggan (1987)
Isle of Man	Jun. - Aug.	SM	Allison (1993)
Isle of Man (Laxey Bay)	Apr. - June Aug. - Sep.	SM, GI, GW	present study
Isle of Man (Port St. Mary)	May. -July	SM, GI, GW	present study
Banty Bay, Ireland	Apr. - May Sep.	SM	Gibson (1956)
Galway Bay, Ireland	Apr. - May July. -Aug.	GI, H, S	Wilson (1987)
Wales, UK	Apr. - May Aug. - Sep.	SM	Baird (1966)
La Rochelle, France	Apr. - May	H	Lubet (1959)
Bay of Brest, France	July - Aug.	GW, GI	Lubet *et al.* (1987a)
Bay of Brest and Bay of St. Brieuc, France	July - Aug.	GI	Paulet *et al.* (1988)
French coast	Apr. -May June, Sep,	SM	Devauchelle & Mingant (1991)
Malaga, Spain	May-July	S	Roman (1991)

SM (staging method), MO (microscopic observation), H (histology), GW (gonad weight), GI (gonadal index), L (larval abundance) and S (spat abundance).

In the Irish Sea most studies have reported two main spawning periods. In Manx waters, the spawning cycle of *P. maximus* has not been studied as frequently as that of *A. opercularis*, although early studies were carried out by Dakin (1909) and Tang (1941). Mason (1958a) produced the most comprehensive work on the biology and the life cycle of the species and gave details of the annual spawning cycle. He observed that two major spawnings occurred yearly in adults, in spring (April - May) and in autumn (August - September), and also noted some genital product release in June. Two similar peaks have also been noted for other inshore populations around the Isle of Man (Duggan, 1987) and for populations off the east coast of Northern Ireland (Stanley, 1967).

In the present study the main spawning of *P. maximus* in Laxey Bay was in the late spring or early summer (April-June) and there was a small but distinct autumn spawning in August-September. In contrast, the offshore Port St. Mary population, like the Scottish and Norwegian populations, only had a single summer spawning peak (in June-July) and there was no evidence of any late summer or autumn spawning in either year. In addition, the development of the gonads and the spawning period itself showed some differences between the two populations. The recovery of the gonads after spawning occurred 1-2 months earlier in the Port St. Mary population, but summer spawning started later, particularly in 1992. Thus full gonads were present for a longer period in the Port St. Mary population, and gonad index and gonad weight was higher for much of the year.

Populations of *P. maximus* from areas further south in the geographical range show considerable local variation in seasonal patterns of

gametogenesis and spawning (Lubet *et al.*, 1987a,b, 1991; Ansell *et al.*, 1991). This is particularly apparent for various populations of *P. maximus* in different part of the English Channel. For example, scallops in the Bay of St. Brieuc on the northern coast of Brittany showed highly synchronous maturation of all individuals in spring leading to a primary spawning in July, and a secondary spawning at the end of August. Recovery of the gonads was then delayed until the following spring (Bergeron & Buestel, 1979; Paulet *et al.*, 1988; Ansell *et al.*, 1988).

In contrast, in the Bay of Brest, which is relatively close to the Bay of St. Brieuc the population showed little synchrony between individuals and there were repeated cycles of maturation of cohorts of gametes throughout the year. Many of these were produced during the winter when the oocytes became atretic and were resorbed rather than spawned (Lubet *et al.*, 1987a, 1987b, 1991). This results in considerable seasonal variation in the quality of gametes produced (Cochard, 1985). Differences have also been observed in egg size, larval life span and the duration of metamorphosis between the Bay of St. Brieuc and the Bay of Brest, highlighting differences in reproductive strategy (Paulet *et al.*, 1988). These differences between populations indicate, not only different responses to the local environment (food availability and temperature) but also genetic adaptation. Other studies of the seasonal spawning cycle of *P. maximus* have also indicated that there are different local variations in the cycle in other areas (for example, the Bay of Seine, and the south coast of England) (Baird, 1966; Connor, 1978; Lubet *et al.*, 1991).

1.4.3 Geographical variation in the spawning cycle of other species

Similar geographical differences in the pattern of spawning have also been frequently recorded in various other species of scallops and other bivalves.

One example is the bay scallop, *Argopecten irradians,* which is found in bays and estuaries along the east coast of North America from Nova Scotia to Florida (Gutsell, 1930; Barber & Blake, 1981, 1983). Studies on the spawning cycle of this species reveal latitudinal trends in the duration of spawning periods, oocyte diameter and fecundity. Spawning commenced in May for the Massachusetts populations (Taylor & Capuzzo, 1983), July in North Carolina (Gutsell, 1930) and September in Florida (Barber & Blake, 1981, 1983). The duration of the spawning period increased with decreasing latitude (Sastry, 1979). The oocyte diameter also decreased further in the southerly direction (Sastry, 1970a; Barber & Blake, 1983). These populations have differing temperature requirements for the initiation of gametogenesis and spawning and, with decreasing latitude, a smaller portion of the overall energy budget is available for gametogenesis, resulting in reduced fecundity (Barber & Blake, 1991).

The sea scallop, *Placopecten magellanicus,* shows geographical differences in both timing and duration of spawning in populations distributed from the Gulf of St. Lawrence to Cape Hatteras on the east coast of North America (MacKenzie *et al.*, 1978). In the area north of Cape Cod, spawning occurs in August and September. Spawning on George Bank occurs in September and in October or October - November

in the mid-Atlantic (MacDonald & Thompson, 1988; Barber & Blake, 1991). Barber & Blake (1991) suggested that, with decreasing latitude, there is a tendency to have twice-yearly spawnings.

Of the numerous examples of other bivalves species, Seed (1976) showed that northern populations of *Mytilus edulis* spawned once in European waters, whereas in southerly waters they spawned twice during their annual spawning period. Bayne (1975), however, showed that thermal or nutritive stress could control the timing of the spawning cycle, the length of the spawning period and the fecundity of *Mytilus edulis* and that the prevalent environmental factors of an area, rather than geographical range, were responsible for affecting the spawning cycle. This was confirmed by a study of the reproductive cycle of five populations of *Mytilus edulis* studied by Newell *et al.* (1982).

The important of temperature in controlling the number of annual spawnings is very well illustrated by the hard-shell clam *Venus mercenaria;* this species was observed to spawn in the spring and autumn when exposed to warmed power station cooling water effluent whereas clams present in cooler water spawn in the autumn only (Mackie, 1986).

The interrelationships between the seasonal spawning cycles of *A. opercularis* and *P. maximus* described in this chapter and the seasonal variations in somatic tissue weights and indices (Chapter 2) and biochemical composition (Chapter 3), will be discussed, together with their synchronisation with environmental factors, in the General Discussion.

CHAPTER 2

SEASONAL VARIATION IN THE SOMATIC TISSUE DRY WEIGHTS AND INDICES OF *AEQUIPECTEN OPERCULARIS* AND *PECTEN MAXIMUS*

2.1 INTRODUCTION

Seasonal variation in body components of bivalves have been studied to determine whether they vary in relation to the spawning cycle in terms of possibly supplying nutrients to the gonads for growth and gametogenesis (Giese, 1969; Sastry, 1979; Gould *et al.*, 1988; Thompson & MacDonald, 1990).

Various bivalve families have been studied such as the Mytilidae, for example, *Mytilus edulis* (Baird, 1957; Lubet, 1959; Dare & Edwards, 1975) and *Modiolus modiolus* (Lent, 1967; Comely, 1978, 1981; Jasim, 1986) and the Ostreidae, *Ostrea edulis* (Walne, 1970) and *Crassostrea glomerata* (Dinamani, 1974)

Similar work has also been carried out on *Tellina tenuis* (Ansell & Trevallion, 1967), *Cardium edulis* (Hancock & Franklin, 1972), *Nucula sulcata* (Ansell, 1974b) *Abra alba* (Ansell, 1974c) and *Macrocallista nimbosa* (Haines, 1976).

For the Pectinidae, *Pecten maximus* (Stanley, 1967; Comely, 1974; Mackie, 1986), *Chlamys septemradiata* (Ansell, 1974a), *Aequipecten opercularis* (Soemodihardjo, 1974: Taylor & Venn, 1979), *Argopecten irradians concentricus* (Sastry, 1979; Barber & Blake, 1981), *Chlamys islandica* (Vahl, 1981a, b), *Placopecten magellanicus* (Gould *et al.*, 1988), *Argopecten circularis* (Villalaz, 1989) and *Placopecten yessoensis* (Chang,

1991) have also been studied. These studies have shown considerable seasonal and regional variabilities to occur in many scallops.

The work described in this chapter set out to investigate in more detail seasonal variations in somatic tissue weights and indices of *Aequipecten opercularis* and *Pecten maximus* from two different areas in Manx waters, in conjunction with studies of the reproductive cycles (Chapter 1) and biochemical composition of the body components (Chapter 3).

2.2 MATERIALS AND METHODS

The regular monthly sub-samples of *A. opercularis* (65 - 70 mm shell length) and *P. maximus* (120 - 130 mm shell length) were taken from Laxey Bay and Port St. Mary (Fig.1.1) as described in Chapter 1. The procedure for obtaining the dry weight of body components (adductor muscle, mantle tissue, digestive gland) of the animals has been described in 1.2.2. Individual tissue component indices were calculated as follows for individual animals and mean values and 95% confidence intervals were calculated (after, Sastry & Blake, 1971; Barber & Blake, 1981; Paulet *et al.*, 1988).

$$\text{Adductor muscle index} = \frac{\text{Dry weight of adductor muscle}}{\text{Dry weight of total tissues}} \times 100$$

$$\text{Mantle tissue index} = \frac{\text{Dry weight of mantle tissue}}{\text{Dry weight of total tissue}} \times 100$$

$$\text{Digestive gland index} = \frac{\text{Dry weight of digestive gland}}{\text{Dry weight of total tissue}} \times 100$$

2.3 RESULTS

2.3.1 *Aequipecten opercularis*

2.3.1.1 Adductor muscle dry weight and index

The adductor muscle was always the largest body component comparatively, but it decreased in weight as gonad development proceeded. The variation in adductor muscle dry weight and index of *A. opercularis* from Laxey Bay and Port St. Mary exhibited marked changes during the two year period (Figs. 2.1 and 2.2). For both sites dry weight was very low in late winter and spring (Fig. 2.1). The adductor muscle then increased in weight during late spring and summer to reach its maximum in autumn. During the first six months of the study period, from May to October 1991, adductor muscle dry weight at Laxey Bay increased from 1.31g to 1.79g (a 38% increase) while, for the same period, samples from the Port St. Mary ground showed a more rapid weight increment from 1.41g to 2.48g (a 79% increase). Mean dry weight values remained stable at the two sites from 20 October to 18 November then declined through the winter and spring.

In 1992, the mean dry weight of adductor muscle reached its lowest level in April for both the Laxey Bay (1.07g) and Port St. Mary (1.36g) populations. Weight was gained gradually during the late spring and summer, Port St. Mary reaching a maximum in October (1.93g) and Laxey Bay samples in November (1.92g). A similar decline was observed at both sites during the winter and spring to reach the lowest levels in March, 1993, of 1.23g at Laxey Bay and 1.09g at Port St. Mary.

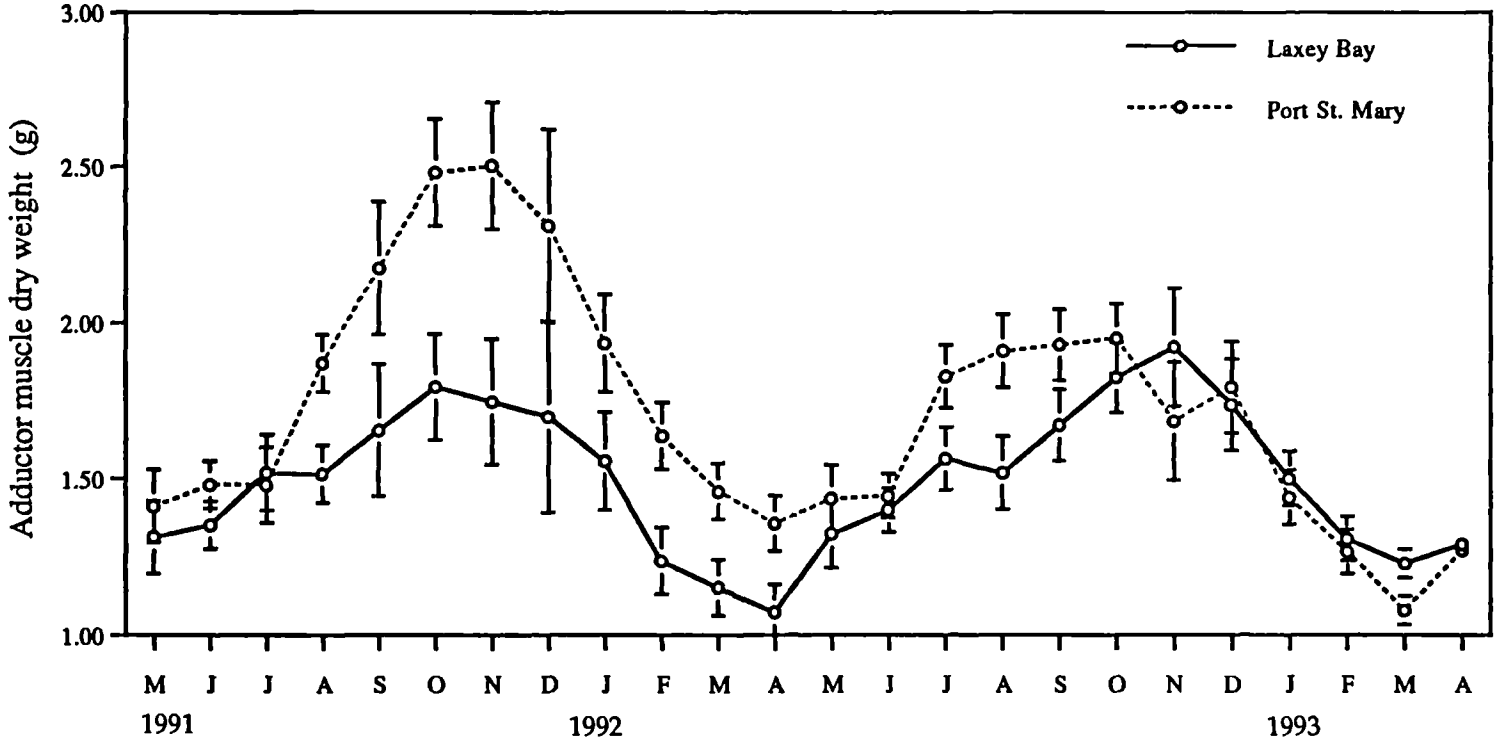


Fig. 2.1. Seasonal variation in the adductor muscle dry weight of *Aequipecten opercularis* (60-70 mm shell length) from Laxey Bay and Port St. Mary . Values represent means with 95% confidence intervals. Error bars smaller than the data points do not appear on the graph (no data available for September 1992 for Laxey Bay).

For almost every month during the period July, 1991 to October, 1992 the mean adductor dry weight was significantly higher (95% confidence level) for the offshore Port St. Mary samples than for Laxey Bay but there were no statistically significant differences in the first three months of the study or from October 1992 till April 1993 (except March 1993).

Adductor muscle dry weight on the Port St. Mary ground built-up to a much higher level in 1991, compared with 1992, indicating a much greater acquisition of energy reserves. There was, however, a difference in the timing of the seasonal oscillations of adductor muscle weight between the two grounds for both years of this study.

Dry adductor muscle indices of *A. opercularis* at the two sites also showed a steady fluctuation similar to the variation of dry weight (Fig. 2.2). When sampling commenced in May 1991 the index for the Laxey Bay population increased from 48% to its maximum of 58% in October, while that for the Port St. Mary population increased from 51% to 59% over the same period. The index then declined, slowly at first, but then more sharply during the winter to minimum levels of 47% at Port St. Mary in March 1992 and 42% at Laxey Bay in April. The adductor muscle index then increased during the late spring and summer to reach maxima of 57% at Port St. Mary in October and 58% at Laxey Bay in November. It then declined at both sites through the winter to minimum levels of 46% in March at Port St. Mary and 44% at Laxey Bay in April.

The adductor muscle index was very variable between individuals in some months as reflected by the high 95% confidence limits in Fig. 2.2

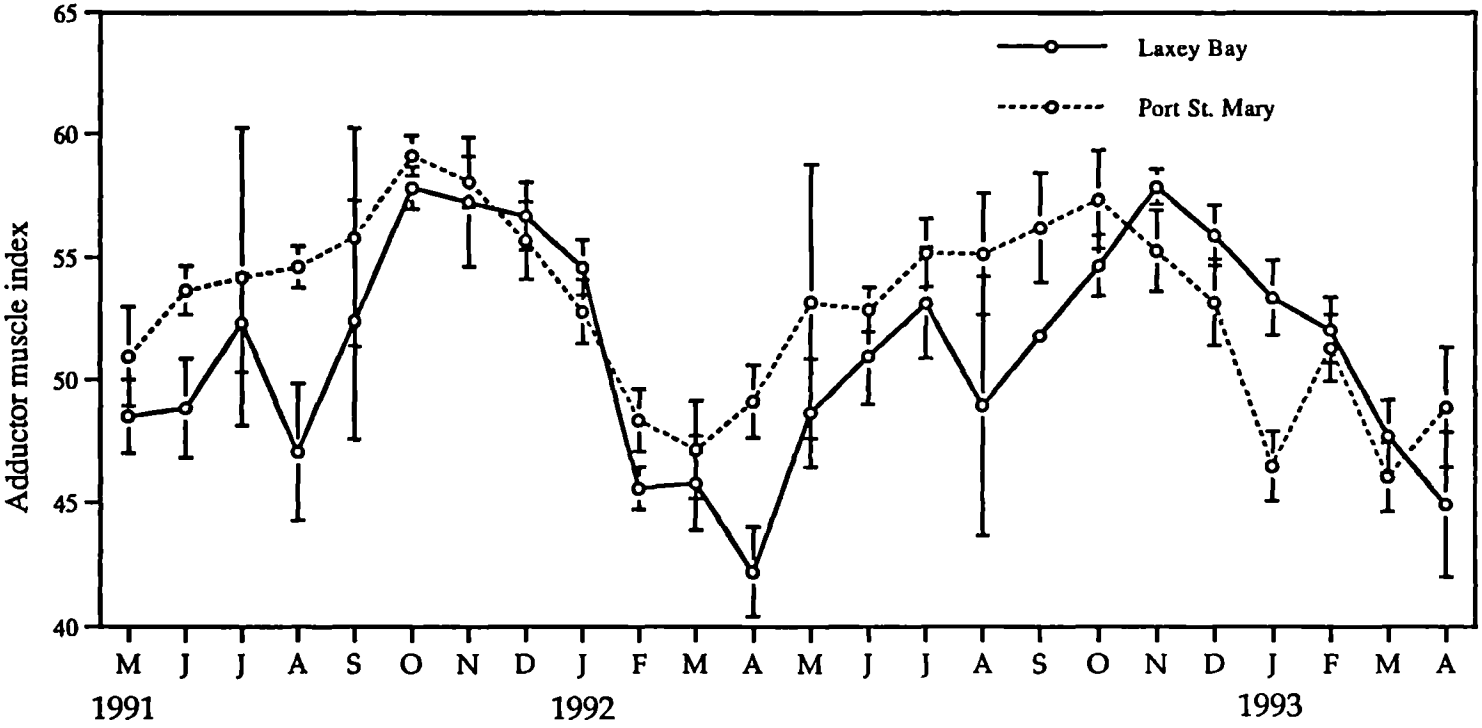


Fig. 2.2. Seasonal variation in the adductor muscle index of *Aequipecten opercularis* (65-70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means with 95% confidence intervals (no data available for September 1992 for Laxey Bay).

but it was generally significantly higher for the Port St. Mary ground during the period when the index was increasing. This reflects a difference in phase, rather than in amplitude of the seasonal oscillations, the index for the offshore Port St. Mary ground starting to increase about one month before that for Laxey Bay population.

2.3.1.2 Mantle tissue dry weight and index

Mean mantle dry weight at both sites generally increased in the period from May to October or November, then decreased through winter and spring (Fig. 2.3). Individual variation was quite large, as reflected by the large 95% confidence limits, so there were few statistically significant differences between the monthly values obtain for the two grounds. However, mean mantle dry weight appeared to build-up to a higher level in 1991 on the Port St. Mary ground, than at Laxey Bay and remained higher though the early part of 1992 but this difference was not repeated through the winter and spring of 1992/93. Mantle tissue indices for the two populations had high 95% confidence limits and showed no clear cyclical trends (Fig. 2.4). They were, however, significantly higher for the Laxey Bay population than for the Port St. Mary population for a few months in 1991.

2.3.1.3 Digestive gland dry weight and index

The mean digestive gland dry weight and index values followed a very similar pattern to the variation of adductor tissue weight and index throughout the period (Fig. 2. 5 and Fig. 2. 6) at the two sampling sites. During the summer they built-up in weight and achieved a maximum in late summer or early autumn. Weight fell in late autumn and winter

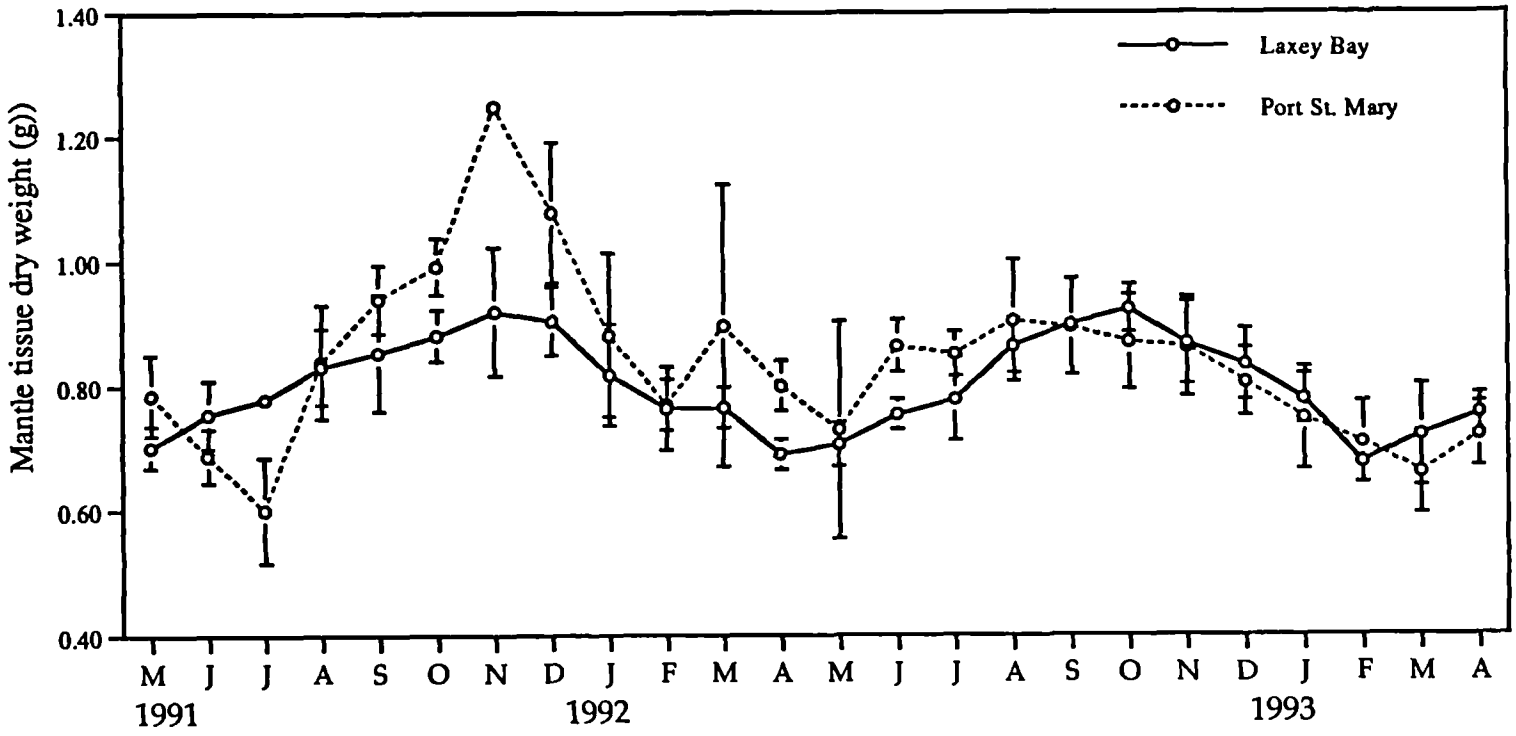


Fig.2.3. Seasonal variation in the mantle tissue dry weight of *Aequipecten opercularis* (65-70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means with 95% confidence intervals. Error bars smaller than the data points do not appear on the graph (no data available for September 1992 for Laxey Bay).

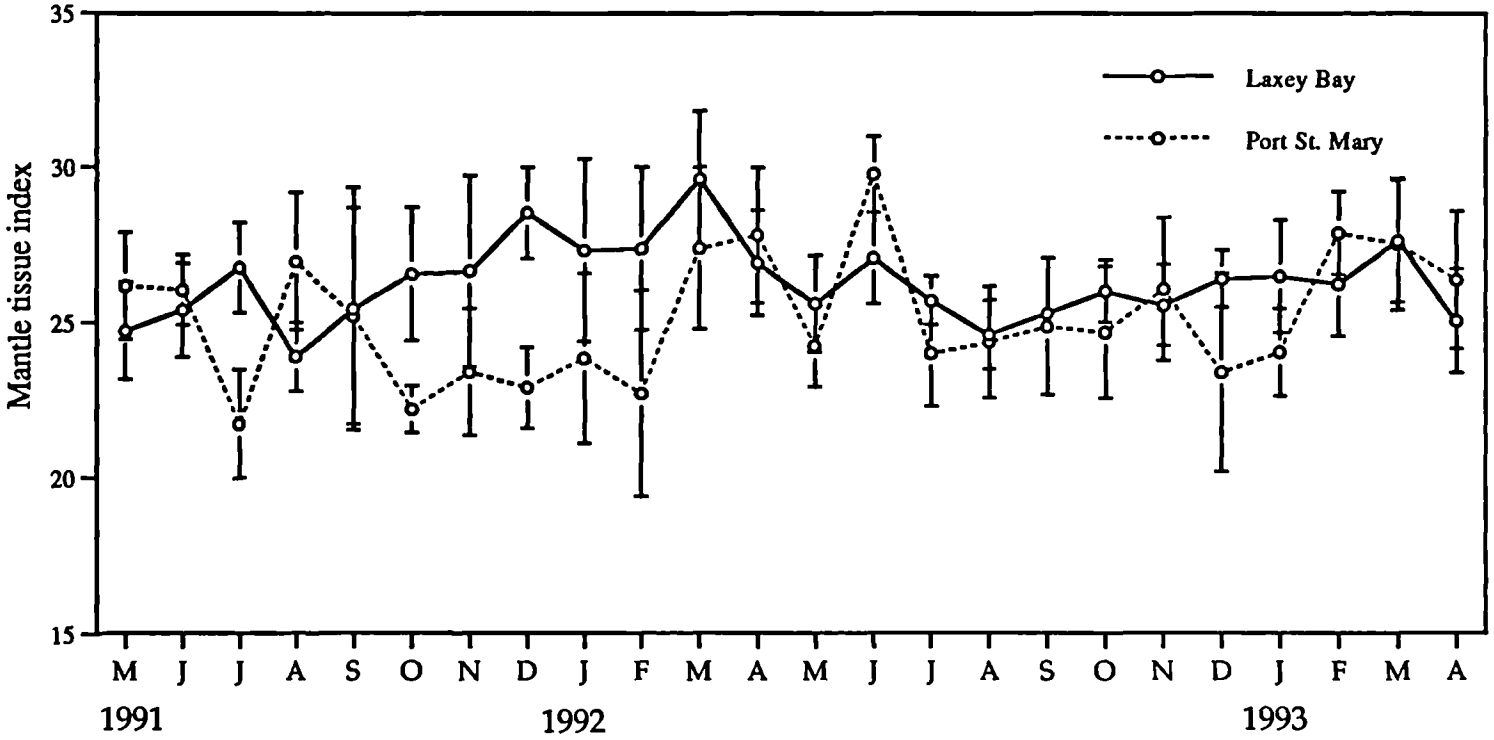


Fig. 2.4. Seasonal variation in the mantle tissue index of *Aequipecten opercularis* (65-70 mm shell length) from Laxey Bay and Port. St. Mary. Values represent means with 95% confidence intervals (no data available for September 1992 for Laxey Bay).

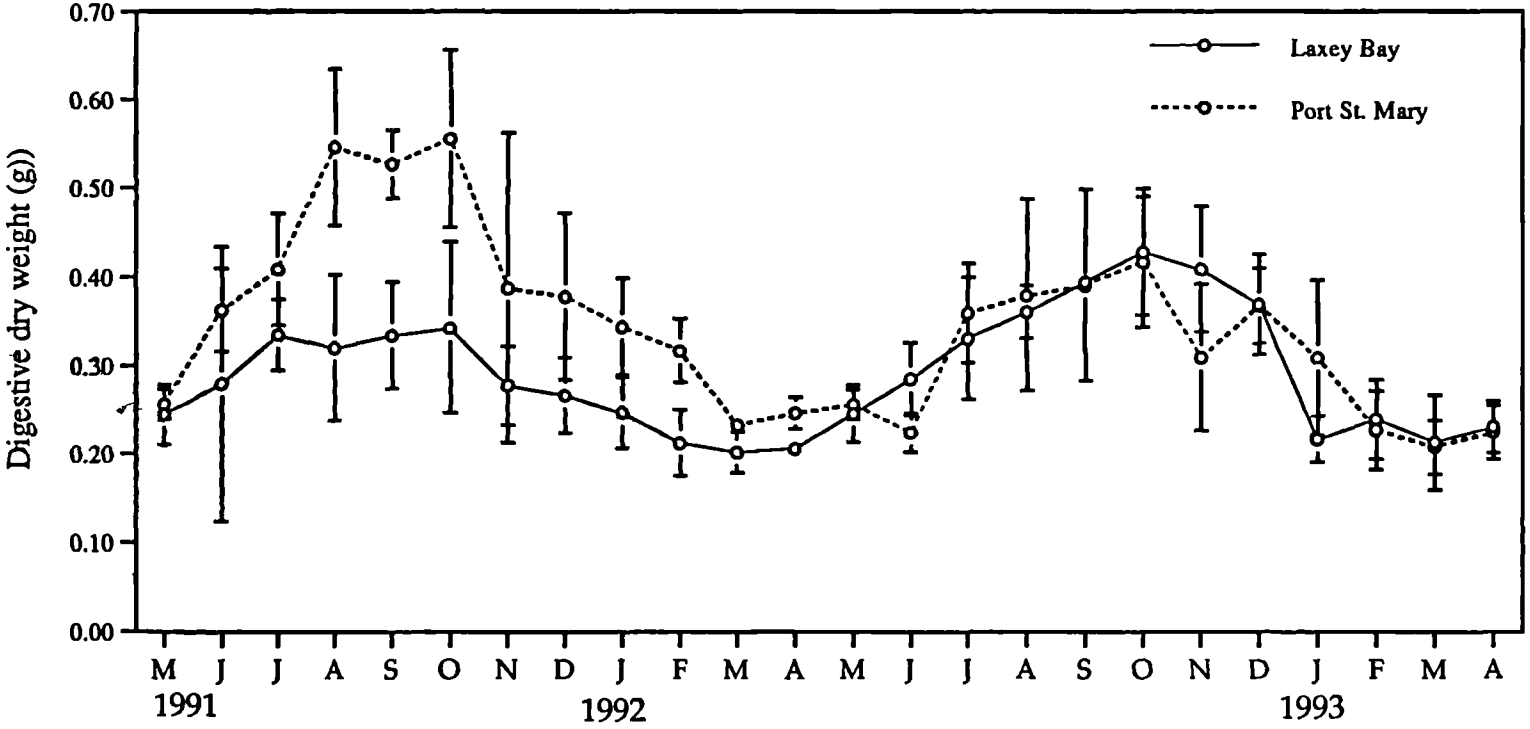


Fig. 2.5. Seasonal variation in the digestive gland dry weight of *Aequipecten opercularis* (65-70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means with 95% confidence intervals (no data available for September 1992 for Laxey Bay).

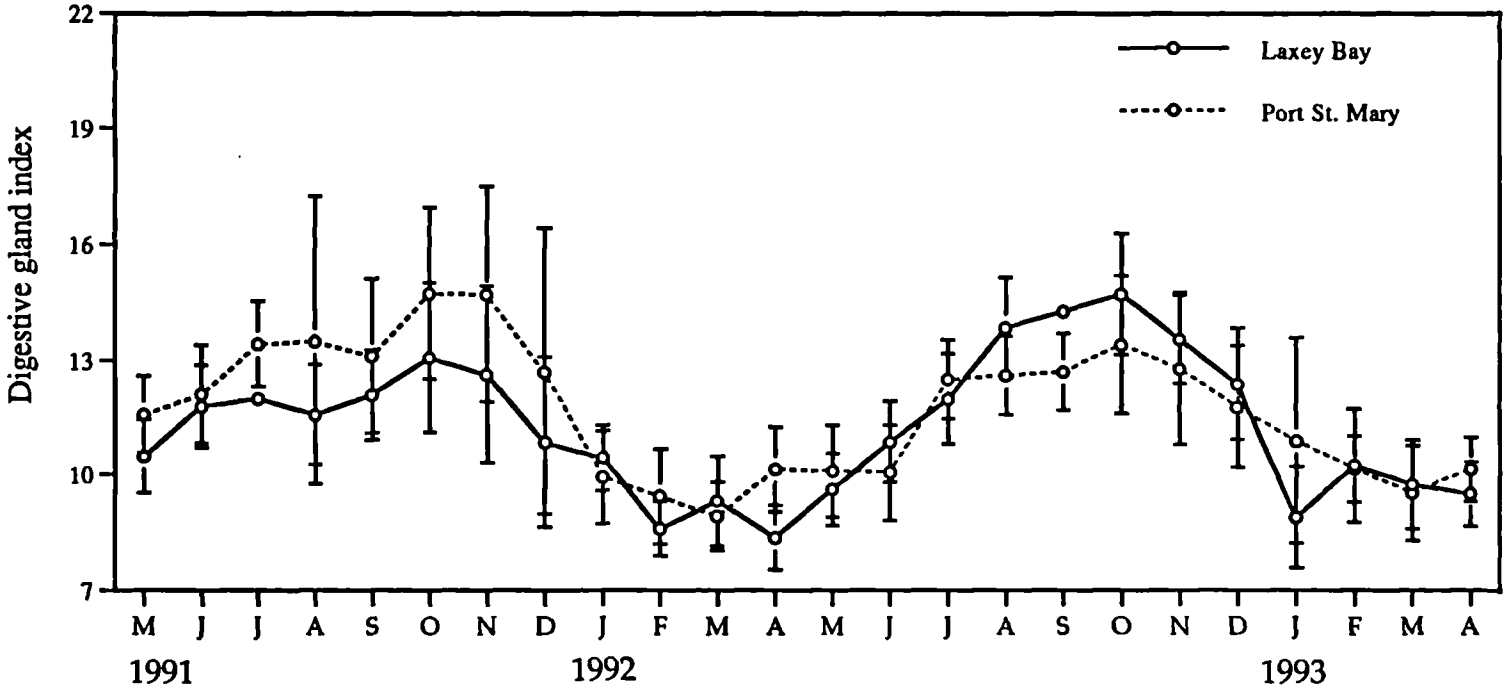


Fig. 2.6. Seasonal variation in the digestive gland index of *Aequipecten opercularis* (65-70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means with 95% confidence intervals (no data available for September 1992 for Laxey Bay).

to reach its lowest level in late winter and early spring. For the Laxey Bay population, weight increased from 0.24g in May 1991 to a maximum of 0.33g in September and October, while the Port St. Mary population increased from 0.26g to 0.56g during the same period. Over the winter, weight declined gradually reaching a minimum of 0.20g in March and April, 1992 for Laxey Bay and 0.23g for Port St. Mary. The digestive gland weight increased over the summer of 1992, both populations reaching their maximum in October (0.43g for Laxey Bay, 0.42g for Port St. Mary). In 1993, both populations reached their lowest level in March (0.21g). It is very clear that for the first half of the experimental period (May 1991 to April 1992) mean digestive weight at the Port St. Mary ground showed significantly higher values (95% confidence level) than for Laxey Bay, but there were no statistically significant differences thereafter.

The digestive gland index also showed a similar pattern of variation to the dry weight throughout the period. It was generally higher for the Port St. Mary population in 1991 and for the Laxey Bay population in autumn 1992 but few of the monthly values were significantly different between the two grounds due to the high 95% confidence limits.

2.3.1.4 Somatic tissue dry weight (adductor muscle, mantle tissue and digestive gland)

The mean monthly values for dry weight of adductor muscle, mantle tissue and digestive gland (Figs. 2.1, 2.3, 2.5) are summed in Fig. 2.7 to show the seasonal fluctuations of total somatic tissue (without gonads).

The dry weight of the somatic tissue of *A. opercularis* from Laxey Bay increased gradually from May 1991 (2.26g) to reach a maximum in

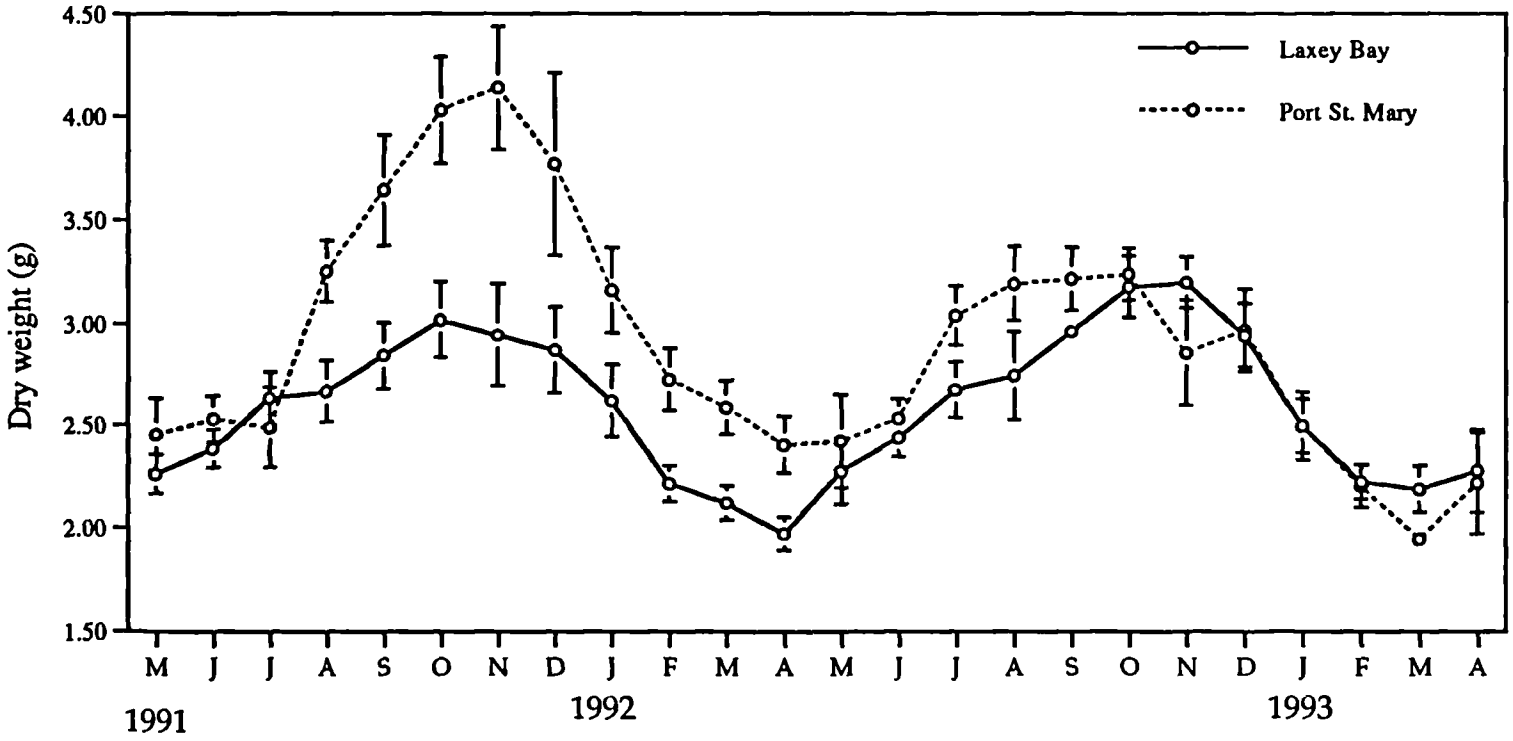


Fig. 2.7. Seasonal variation in the somatic tissue dry weight (adductor muscle, mantle tissue, digestive gland) of *Aequipecten opercularis* (65-70 mm shell length) from Laxey Bay and Port St. Mary ground. Values represent means with 95% confidence intervals. Error bars smaller than data points do not appear on the graph (no data available for September 1992 for Laxey Bay).

October (3.02g). During the same period animals from the Port St. Mary ground showed a much more rapid weight gain from 2.45g to 4.14g in November. They then fell to their lowest level in April, 1992, when samples from Laxey Bay were 1.97g, while those from the Port St. Mary ground were 2.40g. The maximum weight in 1992 for the population from Laxey Bay was reached in November (3.20g), while the Port St. Mary population showed this earlier, in October (3.24g). The dry weight of both populations then decreased during the late autumn and winter to reach their lowest levels again in March, 1993 of 2.19g for Laxey Bay and 1.95g for Port St. Mary. Throughout the period July, 1991 to October, 1992 mean somatic tissue weights were significantly higher (95% confidence limits) for the Port St. Mary population than for the Laxey Bay population but for the final seven months of the study there was no statistically significant difference.

2.3.2 *Pecten maximus*

2.3.2.1 Adductor muscle dry weight and index

Figs. 2.8 and 2.9 show seasonal variations in adductor muscle dry weight and muscle index for populations of *P. maximus* from Laxey Bay and Port St. Mary during the two year period from May 1991 to April 1993. Animals from both sites gained adductor muscle weight gradually from May 1991 to October, then decreased in weight through late autumn and and winter to reach their lowest levels in April and May 1992. Weight then increased, more rapidly at first on the Port St. Mary ground, to reach the maximum levels in October and November, before declining to minimum levels in March 1993. There was some indication of higher adductor muscle values in 1991, compared with 1992, on the offshore Port St. Mary ground and of a phase difference between the cycles on the

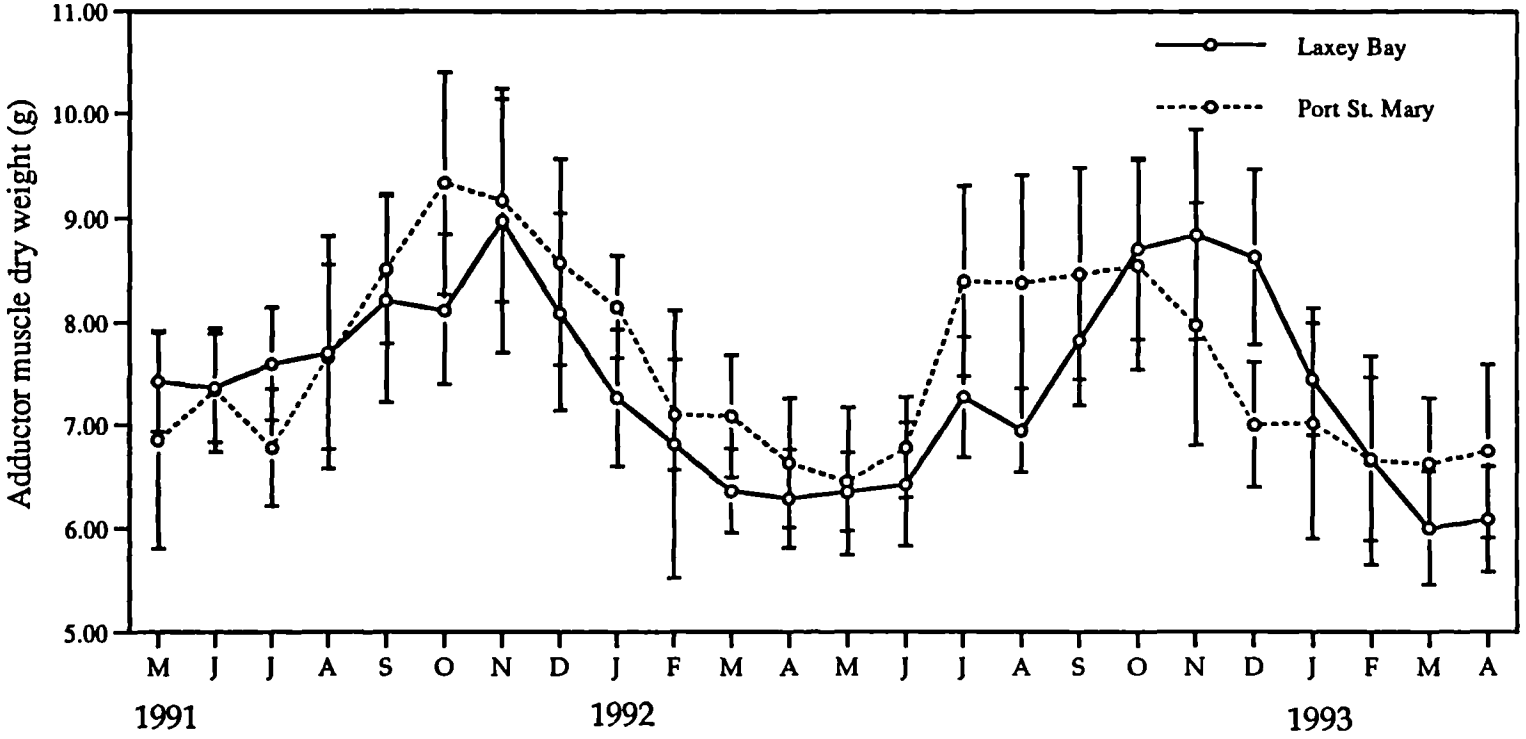


Fig. 2.8. Seasonal variation in the adductor muscle dry weight of *Pecten maximus* (120-130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means with 95% confidence intervals.

two grounds in both years, with the adductor muscle building-up and falling 1-2 months earlier on the Port St. Mary ground than in Laxey Bay. However, individual variability was high, and there were very few statistically significant differences between the monthly values recorded for the two grounds.

The pattern of variation of adductor muscle index for the two grounds (Fig. 2.9) was very similar to that of adductor muscle dry weight. The seasonal cycles were of a similar amplitude on the two grounds but there was a clear indication of a difference in phase, with adductor tissue index falling 1-2 months earlier on the Port St. Mary ground in both years. As a results there were statistically significant differences between the two grounds in late autumn and winter, but for the rest of the year the 95% confidence limits for the monthly samples were overlapping.

2.3.2.2 Mantle tissue dry weight and index

The seasonal variation of mantle tissue dry weight and index showed no obvious pattern throughout the experimental period and individual variability was high (Fig. 2.10 and Fig. 2.11). It is very clear that the mantle tissue does not contribute significantly to the pattern of seasonal changes in total body weight. It was also observed that the mantle tissue contained a large amount of body fluid compared to the other somatic tissues of the scallop.

2.3.2.3 Digestive gland dry weight and index

The cycle of changes of digestive gland dry weight and index showed a similar seasonal pattern to the adductor muscle (Fig. 2.12 and Fig. 2.13).

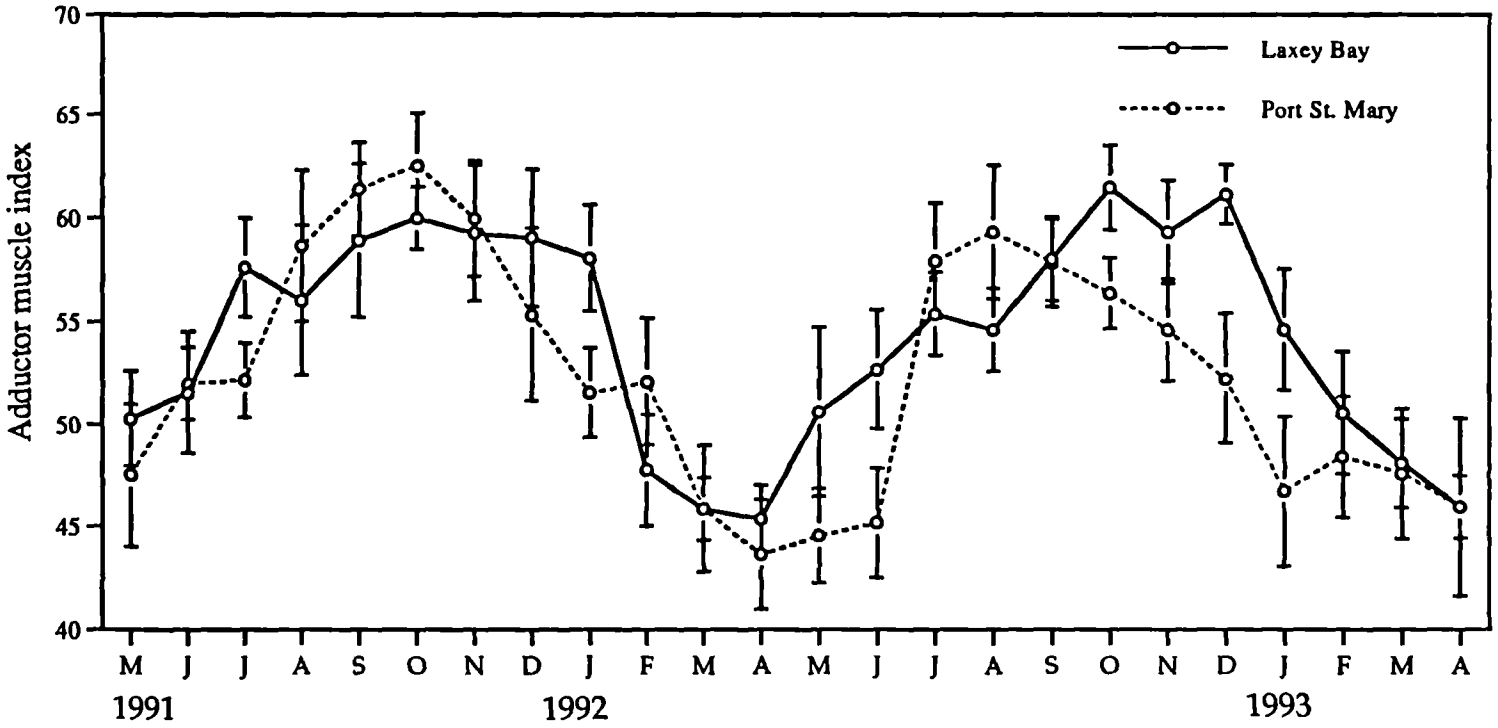


Fig. 2.9. Seasonal variation in the adductor muscle index of *Pecten maximus* (120-130 mm shell length) from Laxey Bay and Port St. Mary. values represent means with 95% confidence intervals.

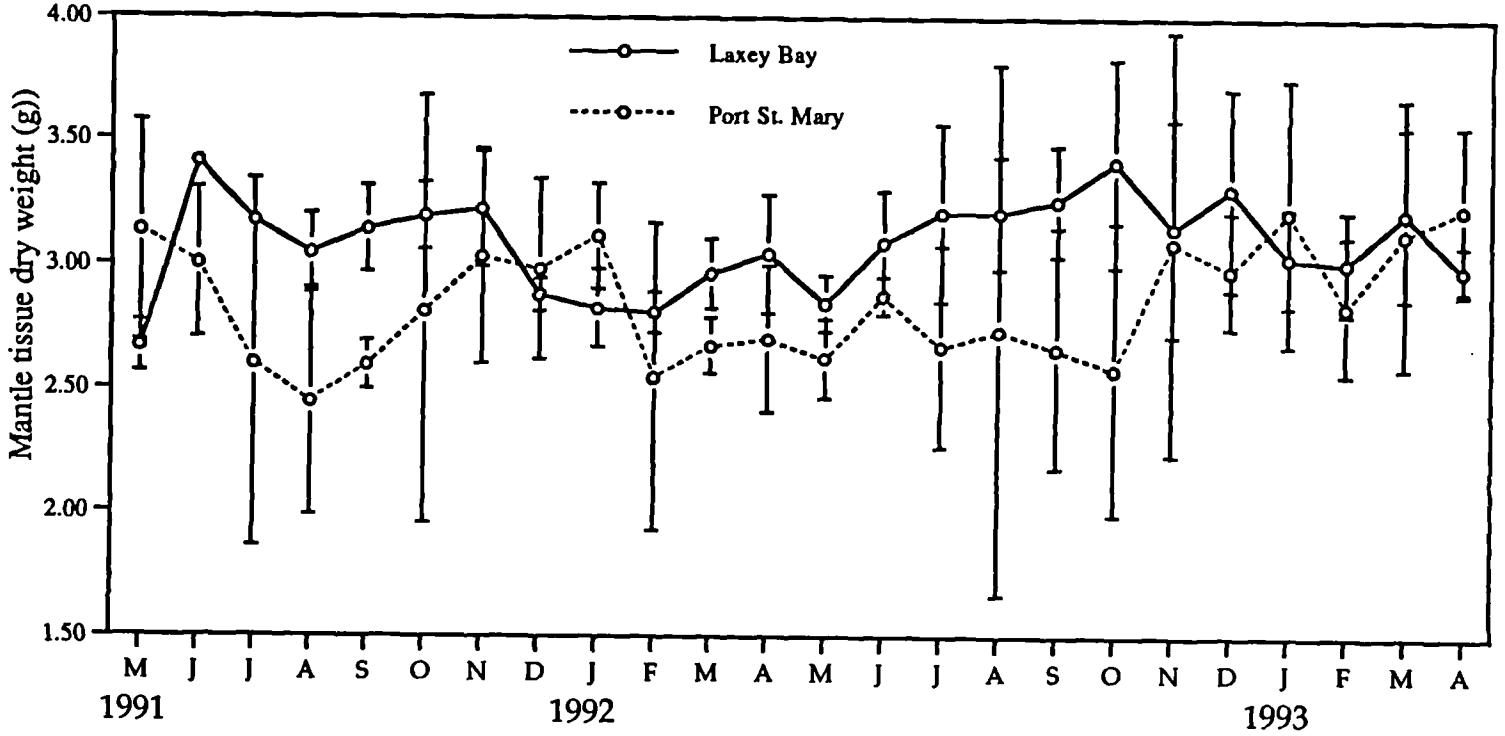


Fig. 2.10. Seasonal variation in the mantle tissue dry weight of *Pecten maximus* (120-130 mm shell lenght) from Laxey Bay and Port St. Mary. Values represent means with 95% confidence intervals. Error bar for July 1991 (Laxey Bay) is smaller than data point and does not appear on the graph.

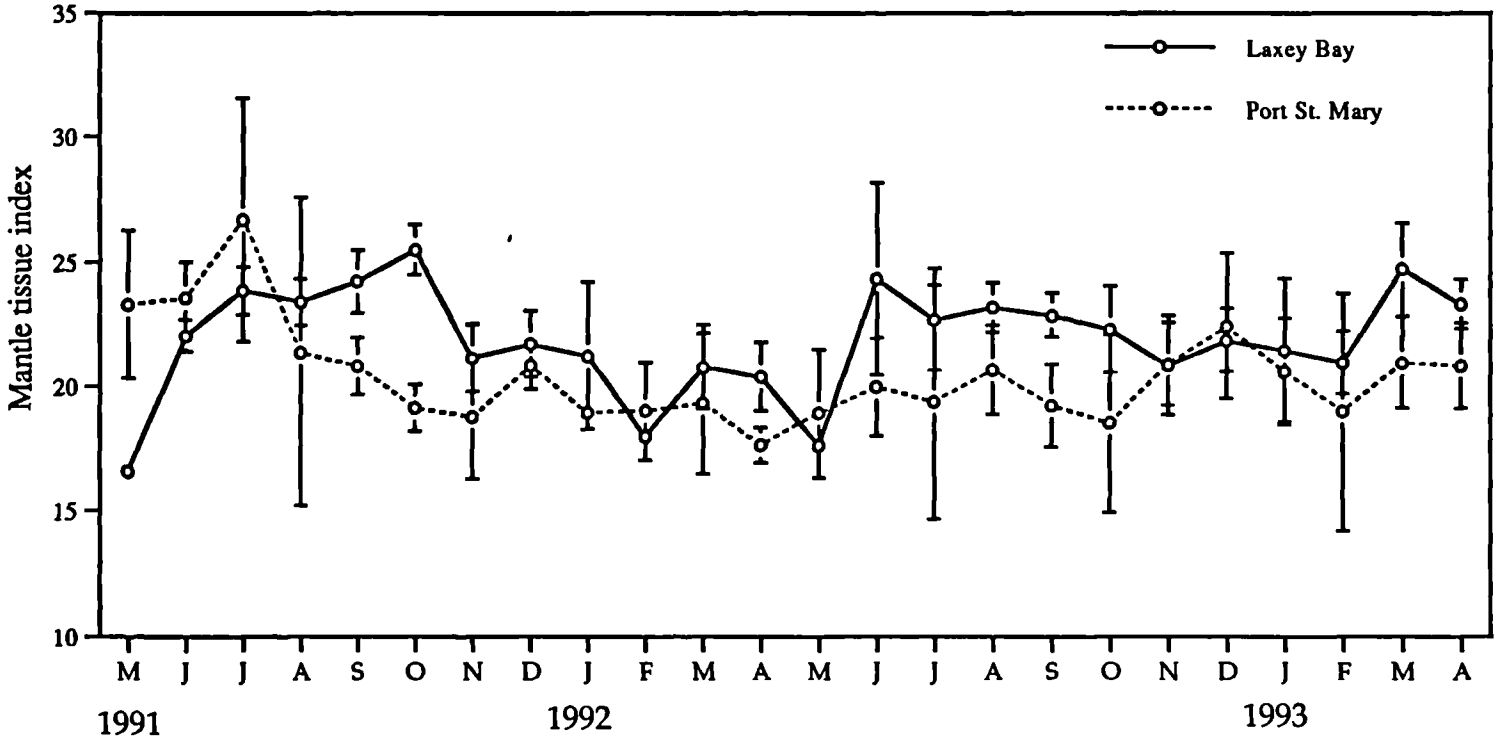


Fig. 2.11. Seasonal variation in the mantle tissue index of *Pecten maximus* (120-130 mm shell length) from Laxey Bay and Port St. Mary ground. Values represent means with 95% confidence intervals.

The mean dry weight of the digestive gland for samples from Laxey Bay (Fig. 2.12) increased steadily through the spring and summer to reach maximum levels in October and November, then declined fairly rapidly to minimum levels in January (1992) and March (1993). For the offshore Port St. Mary samples, the mean dry weight increased very rapidly in May and June to reach its maximum in July and August, after which it declined steady through the autumn and winter to reach minimum levels in March. The seasonal cyle of changes therefore followed a different pattern on the two grounds, being some 3 - 4 months out-of-phase during the period when digestive gland dry weight was increasing. As a result the dry weight for the offshore Port St. Mary samples was significantly higher during July, August and September in both years.

The digestive gland index (Fig. 2.13) fluctuated with a very similar pattern, building-up earlier and to a higher level in August (1991) and July (1992) on the Port St. Mary ground and more slowly to a lower maximum in November (1991) and October (1992) for the Laxey Bay ground. Once again statistically significant differences between samples for the two gound were mostly in the period July - September.

2.3.2.4 Somatic tissue dry weight

The total somatic tissue dry weight was obtained by summing the monthly values for the adductor muscle, mantle tissue and digestive gland. The values obtained for the two grounds (Fig. 2.14) showed a steady cycle of changes throughout the year. Weight increased during the summer when food was abundant in the environment and fell during the winter and early spring as stored food reserves were utilized for gametogenesis and other metabolic activities. The cycle of changes

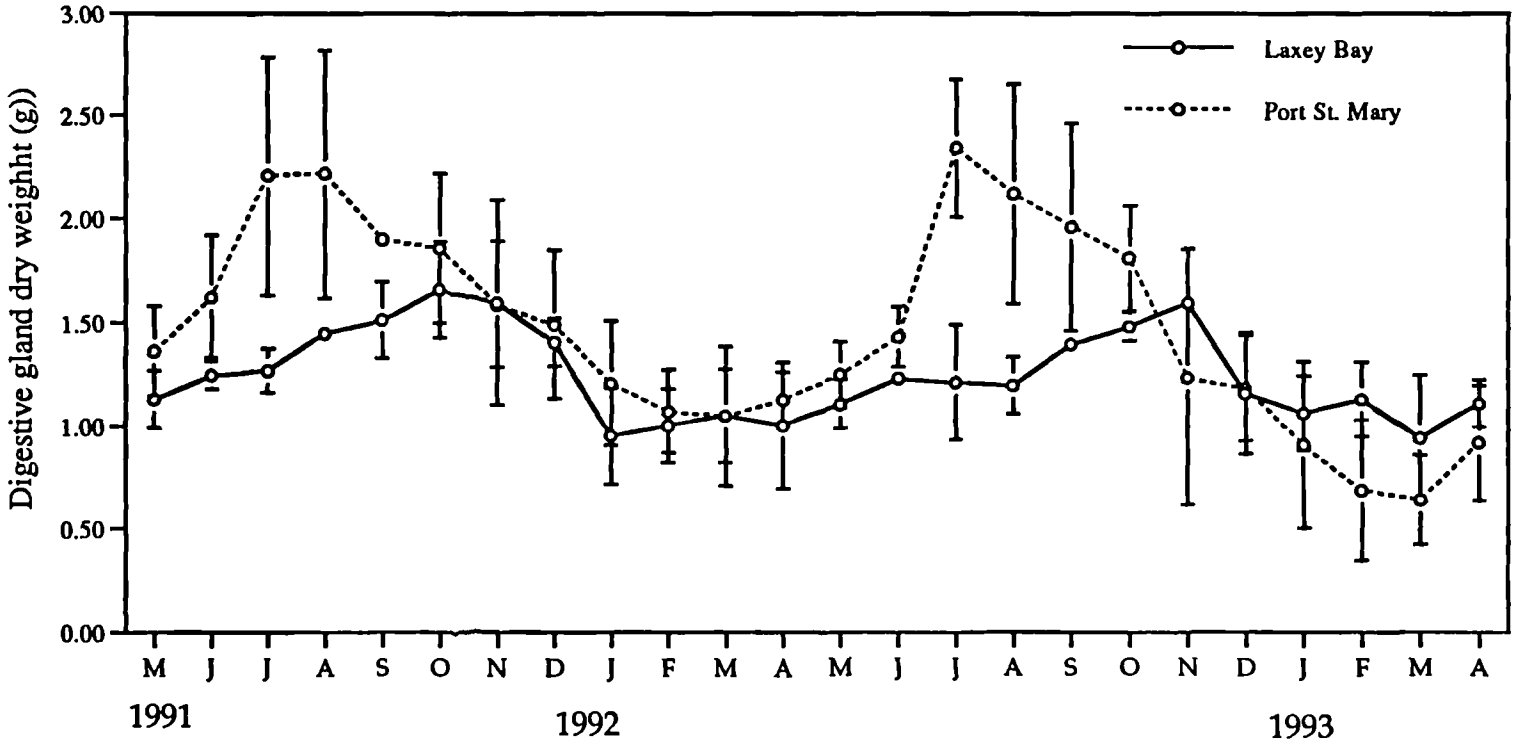


Fig. 2.12. Seasonal variation in the digestive gland dry weight of *Pecten maximus* (120-130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means with 95% confidence intervals. Error bars smaller than the data points do not appear on the graph.

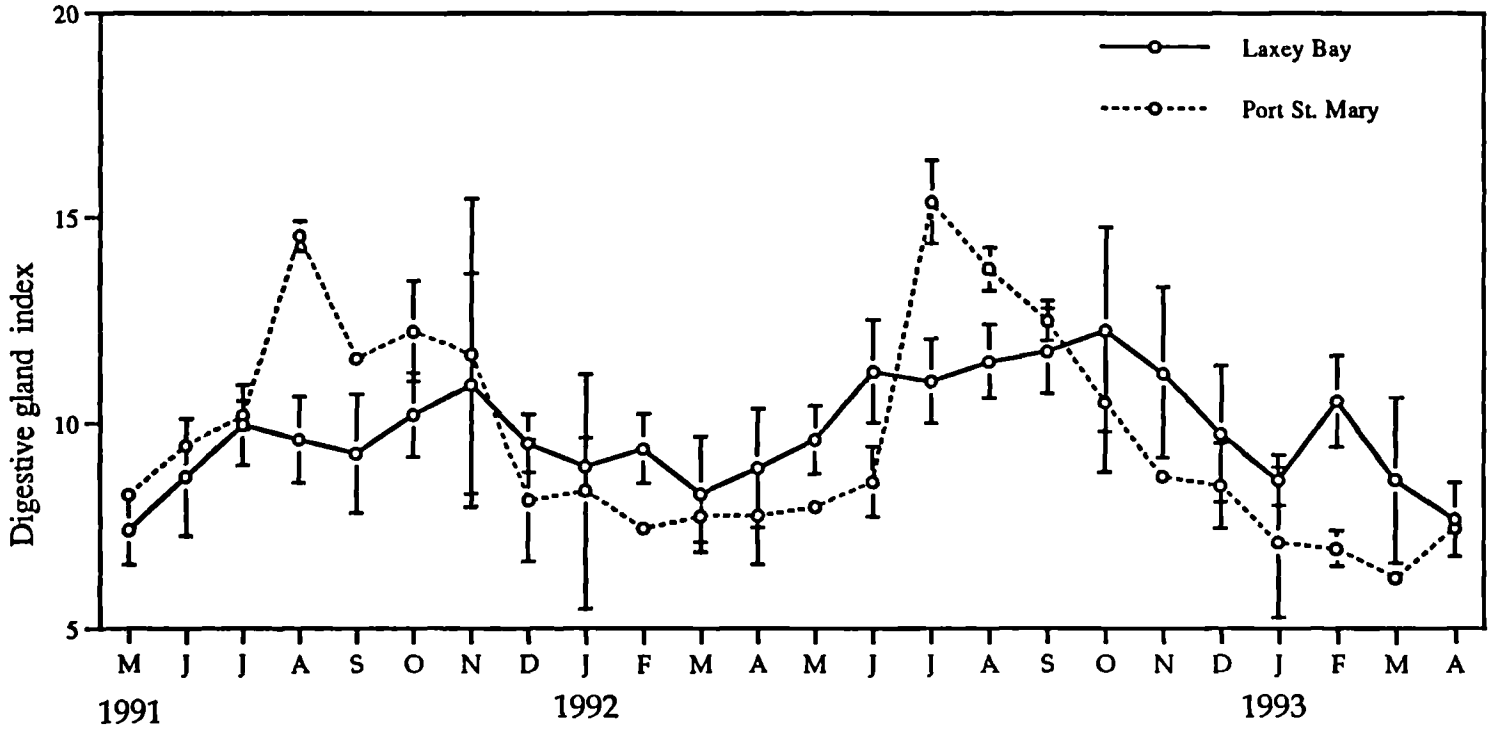


Fig. 2.13. Seasonal variation in the digestive gland index of *Pecten maximus* (120-130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means with 95% confidence intervals. Error bars smaller than data points do not appear on the graph.

was of similar amplitude on the two grounds, with no statistically significant differences between the samples for the two grounds for any months throughout the study. There was, however, some indication of a phase difference between the two grounds during 1992, with total somatic tissue increasing to its maximum and then falling again some three months earlier on the offshore Port St. Mary ground.

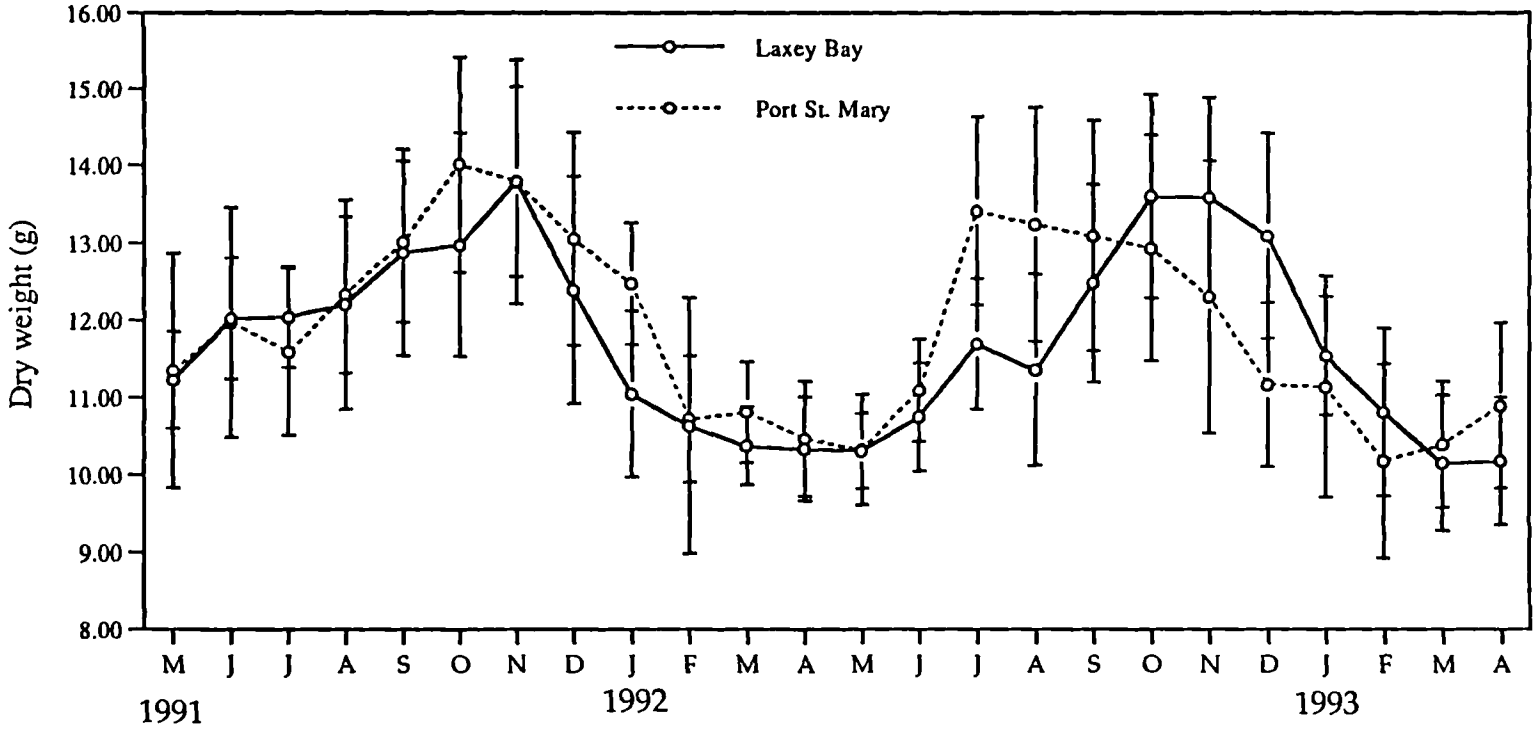


Fig. 2.14. Seasonal variation in the somatic tissue dry weight (adductor muscle, mantle tissue, digestive gland) of *Pecten maximus* (120-130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means with 95% confidence intervals.

2.4 DISCUSSION

The results of the present study show the seasonal changes in the dry weight and indices of the three tissue components (adductor muscle, mantle tissue, digestive gland) of *Aequipecten opercularis* and *Pecten maximus* from the Laxey Bay and Port St. Mary grounds. The tissue weights were at a minimum in spring but increased during the summer to reach a maximum in autumn. These changes relate to the gametogenic cycle (Sastry, 1979; Barber & Blake, 1981) (Chapter 1). The pattern of fluctuation is very similar to that described in previous studies. For example, for *A. opercularis* from Manx waters (Soemodihardjo, 1974) and the Clyde Sea (Taylor & Venn, 1979), and *P. maximus* from the north Irish Sea (Stanley, 1967), the Clyde Sea (Comely, 1974) and from Loch Creran (Mackie, 1986). In *Chlamys septemradiata,* Ansell (1974b) also observed similar fluctuations in these tissues in the Clyde Sea area.

For both *A. opercularis* and *P. maximus* the tissue weights of all the body components were generally significantly higher in the Port St. Mary population, compared with the Laxey Bay population, and this was particularly evident in 1991. It would therefore appear that environmental conditions were not as favourable for the growth of both queens and scallops in the summer of 1992, as they were in 1991.

There was also a clear indication, for both species, that the seasonal cycles of build-up and decline were out-of-phase on the two fishing grounds. This was particularly evident for *P. maximus,* where both the build-up and fall of dry weight occurred 1-2 months earlier in the adductor muscle and 3-4 months earlier in the digestive gland. This phase difference was

not evident in the digestive gland or mantle of *A. opercularis*, but the build-up of the adductor muscle was at least one month earlier in the Port St. Mary population.

The seasonal changes in adductor muscle and digestive gland dry weight are summarised in Figures 2.15 and 2.16, together with the gonad dry weight, for *A. opercularis* and *P. maximus* respectively. These diagrams clearly show the inverse relationships between the gonad dry weight, and both the adductor and digestive gland dry weights, which suggest that reserves stored in these tissues are being utilised in the winter months for gonad growth.

Such changes of tissue weights associated with gametogenesis have been observed on many occasions for different scallop species. For example, Soemodihardjo (1974) described the decrease of muscle weight in *A. opercularis* in Manx waters in winter and spring and attributed this to chemical breakdown of cellular material for gonad development which proceeded steadily in winter, as well as for maintenance of metabolic activities at a time of year when food is scarce. Taylor & Venn (1979), studying *A. opercularis* from the Clyde Sea, observed the lowest dry weight of adductor muscle and digestive gland during spring but they increased in the summer to reach maximum levels in September-October. This increase in weight is associated with changes in the relative amount of protein, carbohydrate and lipid contents in the tissues. Due to gametogenesis during the winter months these reserves reach a minimum by the following spring. In the north Irish Sea (Stanley, 1967), the Clyde Sea (Comely, 1974) and Loch Creran (Mackie, 1986) similar somatic tissue variation was also observed during the gametogenic period of *P. maximus*.

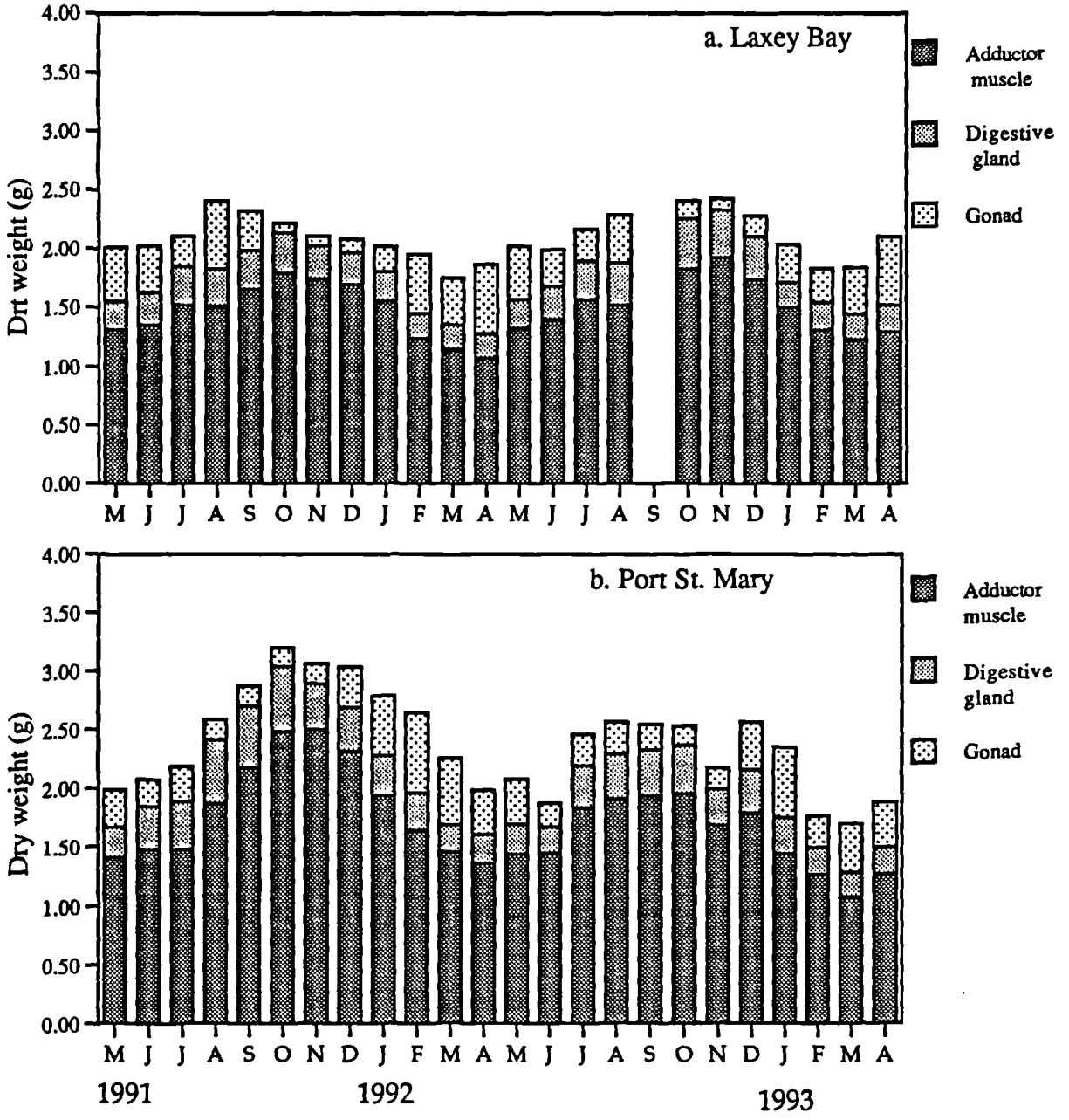


Fig. 2.15. Seasonal variation in the adductor muscle, digestive gland and gonad dry weight of *Aequipecten opercularis* from Laxey Bay (a) and Port St. Mary (b) (no data available for September 1992 for Laxey Bay).

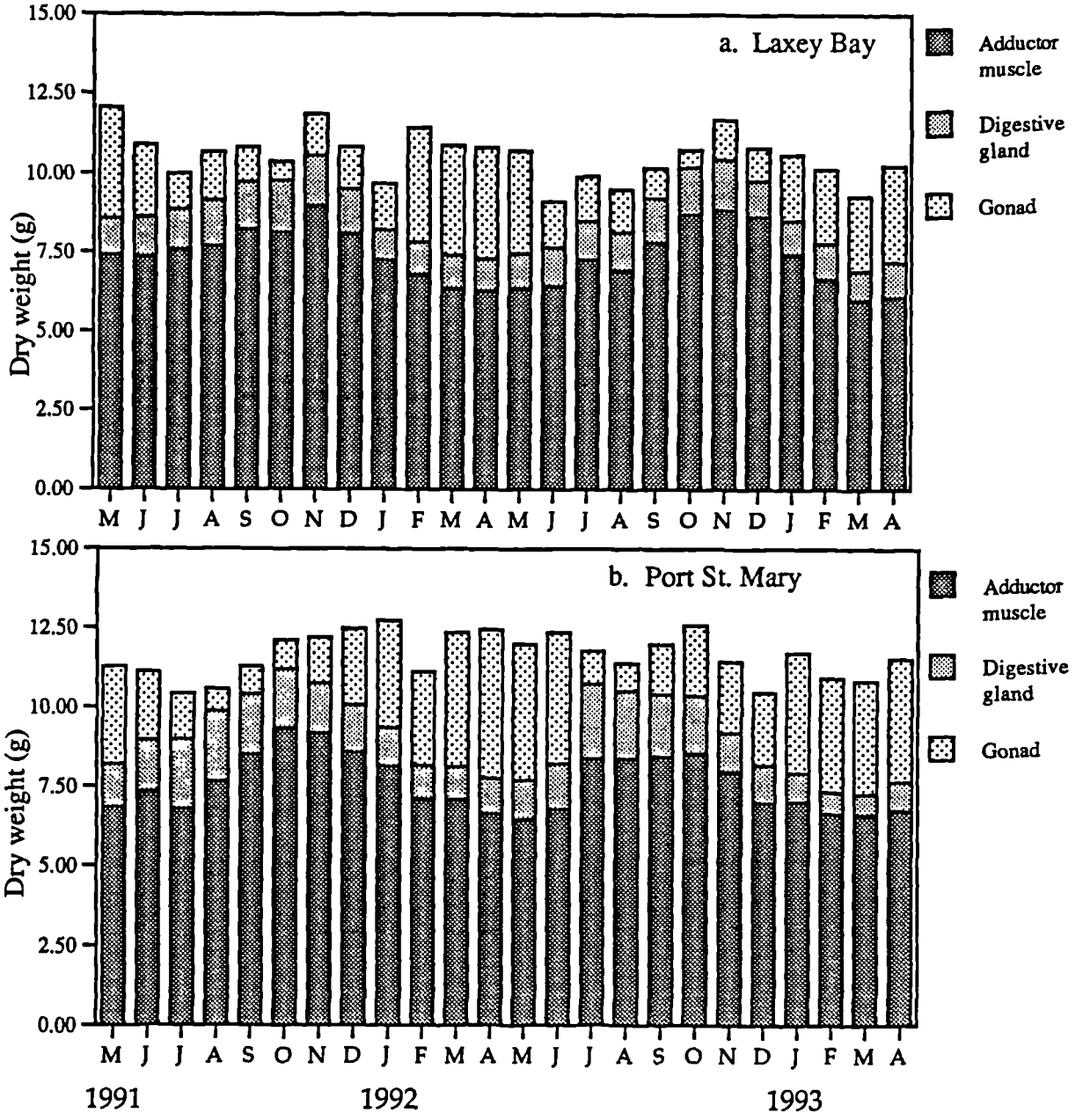


Fig.2.16. Seasonal variation in the adductor muscle, digestive gland and gonad dry weight of *Pecten maximus* (120-130 mm shell length) from Laxey Bay (a) and Port St. Mary (b).

Relative changes in somatic and gonadal material have been observed in other species of pectinid. Ansell (1974b) observed that the weight of the adductor muscle of *Chlamys septemradiata* declined over the winter, reaching a minimum prior to the period of gonad growth. The weight or index of the adductor muscle and digestive gland of *Placopecten magellanicus* decreased in relation to the increase of gonad weight or index (Fugi & Hashizume, 1974; Robinson *et al.*,1981; Schick *et al.*, 1988). Lauren (1982) found that the adductor muscle index of *Hinnites giganteus* was inversely related to the gonad index. This inverse relationship has also been observed in *Chlamys islandica* (Sundet & Vahl, 1981) and *Argopecten irradians* (Hickey 1978; Barber & Blake, 1981) Furthermore, Sastry (1966a) has indicated that a decline in the digestive gland index of *Argopecten irradians* occurs during the period of gonad growth as a result of the rapid transfer of nutrients (lipids) from the ingested food.

The scallop and queen populations in the Irish Sea clearly build-up somatic reserves during the late spring and summer months to be used for the development of the gonads during the subsequent winter. The success of spawning and subsequent recruitment is therefore very dependent on energy reserves acquired the previous year, particularly for populations in which the main spawning period is in the spring or early summer. Seasonal patterns in the build-up and utilisation of protein, lipids and glycogen in different tissues for the Laxey Bay and Port St. Mary populations of scallops and queens are reported in Chapter 3.

The differences in the seasonal cycles of tissue dry weight for the Laxey Bay and Port St. Mary populations of the two species, described above, are

obviously related to differences in the spawning cycle (Chapter 1) and to environmental factors such as temperature and food availability. These will be discussed in detail in the General Discussion.

CHAPTER 3

SEASONAL VARIATION IN ENERGY STORAGE AND UTILISATION IN *AEQUIPECTEN OPERCULARIS* AND *PECTEN MAXIMUS* IN RELATION TO GAMETOGENESIS.

3.1 INTRODUCTION

There has been much interest in the bivalves, stemming in part from their importance as food. This has resulted in much information being collected on a variety of biochemical features of the class. Such biochemical data could be very important for understanding their ecology and overall economy (Giese, 1969; Walne, 1970). These biochemical features and the seasonal changes of tissues are mainly associated with the reproductive cycle (Ansell, 1974; Sastry, 1979; Barber & Blake,1981). Therefore these studies are of particular interest for commercially important species, where the condition of the meat dominates the market value (Giese, 1969; Soemodihardjo, 1974).

Generally in bivalves, energy is stored in tissues in the form of lipid, protein and glycogen (carbohydrate) prior to gametogenesis, when food is abundant in the environment. These substrates are utilised for the production of gametes (Gabbott, 1975; Bayne, 1976a; Ansell, 1978; Gould *et al.*, 1988b). In *Chlamys septemradiata* (Ansell, 1974), *Aequipecten opercularis* (Taylor and Venn, 1979) and *Pecten maximus* (Stanley, 1967; Comley, 1974) declines of adductor musle weight are accompanied by decreases in protein and glycogen content and increase in gonadal lipid. Comely (1974) showed that adductor muscle food reserves in *P. maximus* are utilised during food shortage in the environment, when glycogen provides metabolic energy,

while protein is utilised for gametogenesis. Glycogen stored in adductor muscles during the summer in *Chlamys islandica* was depleted during the winter (Sundet & Vahl, 1981). In *Chlamys hericia,* the lipid in the digestive gland is converted into fatty acid and glycerol and then transferred to the gonads (Vasallo, 1973). The digestive gland is known to be a site of storage of lipid in bivalves (Nakazima, 1956; Owen, 1966; Giese, 1969).

Some work has been carried out to study, in greater detail, the mechanisms by which nutrients are stored and utilised (Sastry & Blake, 1971; Gabbott, 1975; Lubet *et al.*, 1987; Faveris & Lubet, 1989). This has involved assaying for the enzymes required in various metabolic pathways (Bennet & Nakada, 1968; Goudsmit, 1972; L-Fando *et al.*, 1972; Gabbott, 1976) and the application of histochemical methods to determine the location of storage products within the tissues of the animal (Eble, 1969), especially with respect to gametogenesis (Eurenius, 1973; Gabbott, 1976; Robinson *et al.*, 1981; Lowe *et al.*, 1982).

Three mechanisms are involved in the reproductive energy metabolism of these pectinids (Barber, 1984; Barber & Blake, 1991). The first mechanism involves the direct transfer of either stored or recently ingested fatty acid from the digestive gland to developing oocytes in the gonad. The second involves the conversion of glycogen to lipid in a manner similar to the glycogen-fatty acid cycle in vertebrates (Gabbott, 1975). A general loss of glycogen reserves from adductor muscle often accompanies lipid accumulation in the gonad (Mori, 1975; Pollero *et al.*, 1979; Robinson *et al.*, 1981). The third mechanism involves the breakdown of protein in major tissues especially the adductor muscle, to support gametogenesis during the winter and early spring (Barber & Blake, 1981; Sundet & Lee, 1984).

In general, studies on energy storage and utilisation are concerned with the way in which the major biochemical constituents (protein, lipid, glycogen) of the tissues change seasonally in relation to growth and reproductive state and this has been the suggestion taken in this study. The body components of two populations of *Aequipecten opercularis* and *Pecten maximus* were analysed biochemically throughout two years for two different grounds where environmental conditions differed, and related to seasonal cycles in the gonads and other body tissues.

3.2 MATERIALS AND METHODS

3.2.1 Preparation of tissues

Samples of *A. opercularis* and *P. maximus* were collected at monthly intervals from the two sites described in Chapter 1. Ten to fifteen animals of each species were selected for the analysis. The range of shell length in each sample was 65 - 70 mm and 120 - 130 mm for *A. opercularis* and *P. maximus* respectively. The soft tissues were removed and dissected into four components, namely, gonad, adductor muscle, mantle tissue and digestive gland. The tissues were rinsed in distilled water to remove surface seawater. Then the samples were weighed and placed in pre-dried aluminium containers and stored in a cold room for freezing. Once the samples were frozen, they were transferred into a freeze-drier (Chem Lab Instruments Ltd SB4) and left until they had reached a constant weight. The dry weights were determined using an analytical balance. The gonads were separated into male and female portions and then individual tissues were ground into powder form using a homogenizer. The powdered samples were placed in sealed plastic vials and stored. Depending upon the gonadal stages, some gonad portions were pooled and powdered to obtain an adequate quantity for the analysis.

3.2.2 Analysis of protein

The Kjeldahl method has been the standard technique for nitrogen determinations of biological materials for many years because it determines nitrogen contents of such materials more effectively than any other method (Giese, 1967). In this procedure the nitrogen in a tissue is converted to

ammonium sulphate by boiling in concentrated sulphuric acid in the presence of a catalyst such as copper sulphate and selenium or mercuric oxide (Lang, 1958).

For the determination of protein, 40 mg was taken from each freeze-dried sample and accurately weighed on Rizla cigarette papers before being placed in Kjeltec digestion tubes (duplicate samples were taken). Ready-made catalyst tablets were added to each tubes as follows :-

1. Kjeltabs ST.
   (3.5g copper sulphate K_2SO_4 and 0.005g
   0.005g selenium Se)
2. Kjeltabs TCT.
   (3.5g potassium sulphate K_2SO_4
   0.105g copper sulphate $CuSO_4 .5H_2O$
   0.105g titanium dioxide TiO_2)

10 ml of concentrated H_2SO_4 were then added to the tube by means of a mechanical dispenser. Six tubes at a time were placed in a preheated aluminium digestion block at 400 °C (Fig. 3.1). Suction cups were fitted to the tubes and the water pump turned on to remove acidic fumes. The samples were left to digest for 25 minutes, by which time the contents of the tubes became completely clear green. Without removing the suction cups the tubes were taken to a stand beside the fume cupboard and allowed to cool for 20 minutes. Next 50 ml of distilled water were added slowly and swirled gently. A cloudy precipitation was observed. One digestive tube at a time was introduced into the Kjeltec System 1002 Distilled Unit. 40 ml of (10M) NaOH were dispensed into the sample through teflon steam tubing. A conical flask containing 25 ml of 4% boric acid solution with 1%

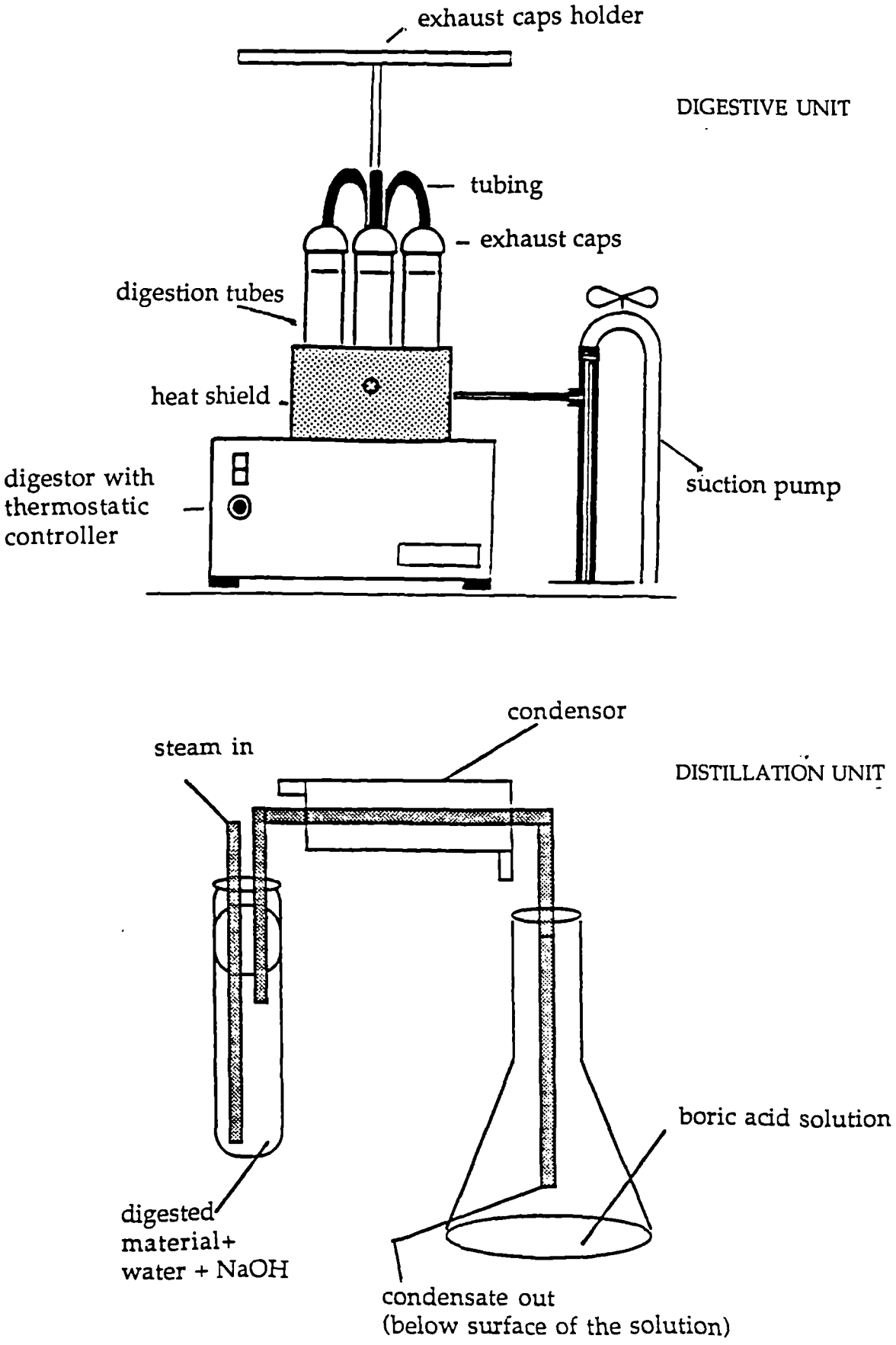


Fig. 3.1. Kjeldahl digestion system.

bromocrysol green and 0.7% methyl red as indicators was placed under the condenser tube. The flask was then raised on the platform so the tip of the tube was below the level of boric acid solution and the steam supply turned on. The steam was switched off once the level in the boric acid reached 100 ml, which was generally after five minutes. The colour of the boric acid solution turned from pink to blue-green. Blanks were prepared using all the reagents and cigarette paper but without the tissue components.

A colour control solution was prepared for the accurate detection of the titration end point. A 50 ml volume of distilled water was transferred into a digestion tube, 40 ml of (10M) NaOH was then added and the solution distilled, as above, into a titration flask containing the 25 ml of boric acid solution to reach 100 ml as above. The colour was typically dull grey. Further boric acid solutions (samples and blanks) were titrated with 0.05M HCl until the colour equated exactly with that of the colour control solution to get the end point.

If 1 ml of 0.05M HCl corresponds to 0.7 mg of nitrogen in the sample, the percentage nitrogen can be calculated from :-

$$\% \text{ nitrogen (\% N)} = \frac{(\text{ml HCl - ml HCl for blanks}) \times 0.7 \times 100}{\text{sample size in mg}}$$

% Protein = % nitrogen x 6.25 (Giese, 1967; Rigby, 1990; Dicky-Collas, 1991).

3.2.3 Analysis of total lipid

The total lipid of the tissues was determined by using the charring method (Rigby, 1990; Dicky-Collas, 1991). The methodology was based on that of Marsh & Weinstein (1966) and Holland and Hannant (1973). The method of chloroform-methanol extraction followed that of Folch *et al.*, (1957). The main advantages of this procedure are its rapidity and sensitivity. In addition, concentrated sulphuric acid is employed as a single reagent (Marsh & Weintein, 1966).

Freeze-dried tissue powder (20 mg) was placed into a narrow-bottomed centrifuge tube and 1 ml of 1:2 chloroform: methanol added. This sample was gently shaken and another 1 ml of the solvent was added to wash down the sides of the tube. The tubes were covered and left at 4°C in a refrigerator for 20 minutes to extract the lipid. Then 0.8 ml of methanol was added to each sample to reduce the specific gravity of the two layers which could be seen in the samples. Centrifugation was carried out at 800 R.P.M. for 10 minutes to removed the solid particles from suspension. The supernatant was transferred into a teflon-lined screw cap tube by using disposable Pasteur pipettes. Then 0.8 ml of chloroform and 0.64 ml of distilled water were added, samples capped, shaken and again centrifuged for 10 minutes at 800 R.P.M. The lower chloroform layer contained the lipid while the upper level was a methanol-water mixture. This phase was removed by using a suction pump. The remaining lower layer was dried at 100°C for 30 minutes in an oven (caps were removed).

The samples were left to cool in a fume cupboard, then 1 ml of chloroform was added. For the determination of the total lipid, three 50 µl aliquates

were taken from the sample and placed in disposable 3 ml glass vials. Again samples were dried at 100 °C for 20 minutes in an oven. After cooling, 0.5 ml of concentrated sulphuric acid was added slowly along the tube wall, using micropipettes. The vials were then shaken and heated at 200 °C for 15 minutes in a muffle furnace. Once cooled, 2.5 ml of distilled water was added, shaken and cooled again before transferring to disposable cuvettes with a 1 cm path length.

The absorbance of the samples was read at 375 nm on a Philips PU 8670 VIS/NIR spectrophotometer. The lipid was determined by a comparision with a calibration curve created using tripalmitin as a standard. The stock solution was 0.1 g of tripalmitin in 100 ml of chloroform which made a series of dilutions. Triplicate samples were treated by the charring method and the absorbance read at 375 nm. The blank sample was prepared by using 0.05ml of concentrated sulphuric acid and 2.5 ml of distilled water for the initial reading.

3.2.4 Analysis of glycogen

The determination of glycogen was made using the phenol-sulphuric acid method (Dubois *et al.*, 1956; Barber and Blake, 1981). In this method, glycogen gives an orange-yellow colour and it would appear stable and simple for regular analysis (Giese,1957). Three 2-3 mg amounts from each sample were weighed accurately and placed in a labelled test tube. Next 2 ml of distilled water, 1 ml of 5% phenol in distilled water and 5 ml of concentrated sulphuric acid were added, using micro-pipettes. The sample was swirled smoothly and placed in a fume-cupboard for 30 minutes to cool. The contents of the samples were then tranferred into disposable cuvettes with a 1 cm path length. The optical density of the orange-yellow

solutions was read at 490 nm on a Philips PU 8670 VIS/NIR spectrophotometer. A calibration curve was created using 100 mg oyster glycogen in 100 ml of distilled water as a standard. For both samples and standard solutions, the measured extinction was corrected with that of a blank solution. This solution was prepared using 2 ml of distilled water, 1 ml 5% phenol in distilled water and 5 ml of concentrated sulphuric acid.

The data on the biochemical composition of the tissues are presented both in terms of percentage composition and absolute contents of 65 - 70 mm and 120 - 130 mm shell length individuals of *A. opercularis* and *P. maximus* respectively. The absolute content was calculated by multiplying the average percentage composition by the mean component dry weights (see example, Giese, 1969; Ansell, 1974; Comely, 1974; Taylor & Venn, 1979; Barber & Blake, 1981; Couturier & Newkirk, 1991). The calculated data are tabulated and shown in Appendices 3.1 - 3.20.

3.3 RESULTS

3.3.1 Biochemical composition of *Aequipecten opercularis*

3.3.1.1 Adductor muscle

a. Protein

The percentage composition and the absolute content of protein in the adductor muscle of samples from the two populations is shown in Figs. 3.2a and 3.2b respectively. The percentage protein (Fig. 3.2a) was generally at its highest in March and fell rapidly in summer to a low level in autumn, before rising again in winter. The percentage protein was considerably higher for the Laxey Bay population, than for the Port St. Mary population, throughout the autumn and winter of 1991/92 and this was repeated in the winter of 1992/93. In both years these differences were statistically significant ($p < 0.05$) throughout these periods.

The seasonal cycles in the protein content of the average adductor muscle were equally well-marked but differed in both timing and relative amplitude (Fig. 3.2b). In the first year of study (1991-1992), protein contents were highest in October (Laxey Bay) or November (Port St. Mary), then fell to their lowest levels in April 1992 (both grounds). In the second year of study (1992-1993) protein content was highest in November at Laxey Bay but was some three months earlier at Port St. Mary. In marked contrast to the percentage protein composition (Fig. 3. 2a), the actual protein content in 1991 was considerably higher for the offshore Port St. Mary ground, than for Laxey Bay (Fig.3.2b), though the maxima attained at the two grounds were very similar in 1992. The seasonal pattern of change in protein content of

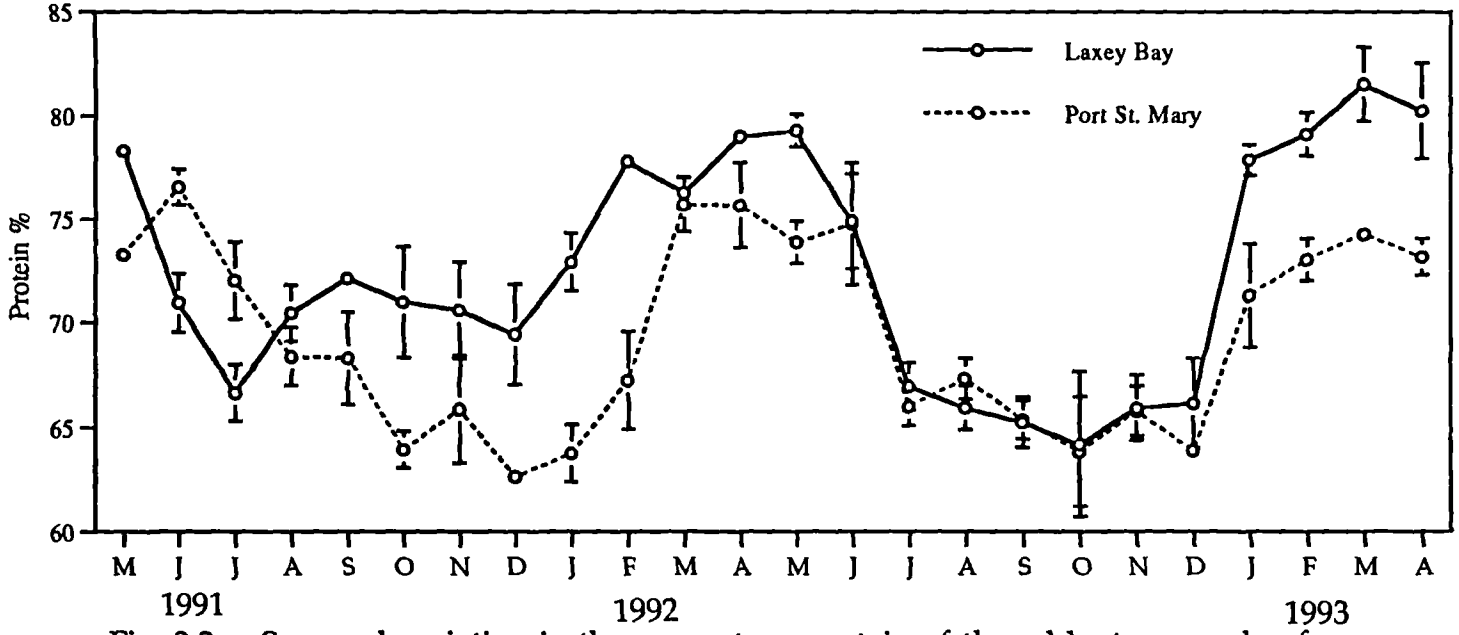


Fig. 3.2a. Seasonal variation in the percentage protein of the adductor muscle of *Aequipecten opercularis* (65-70 mm length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n =10 - 15).

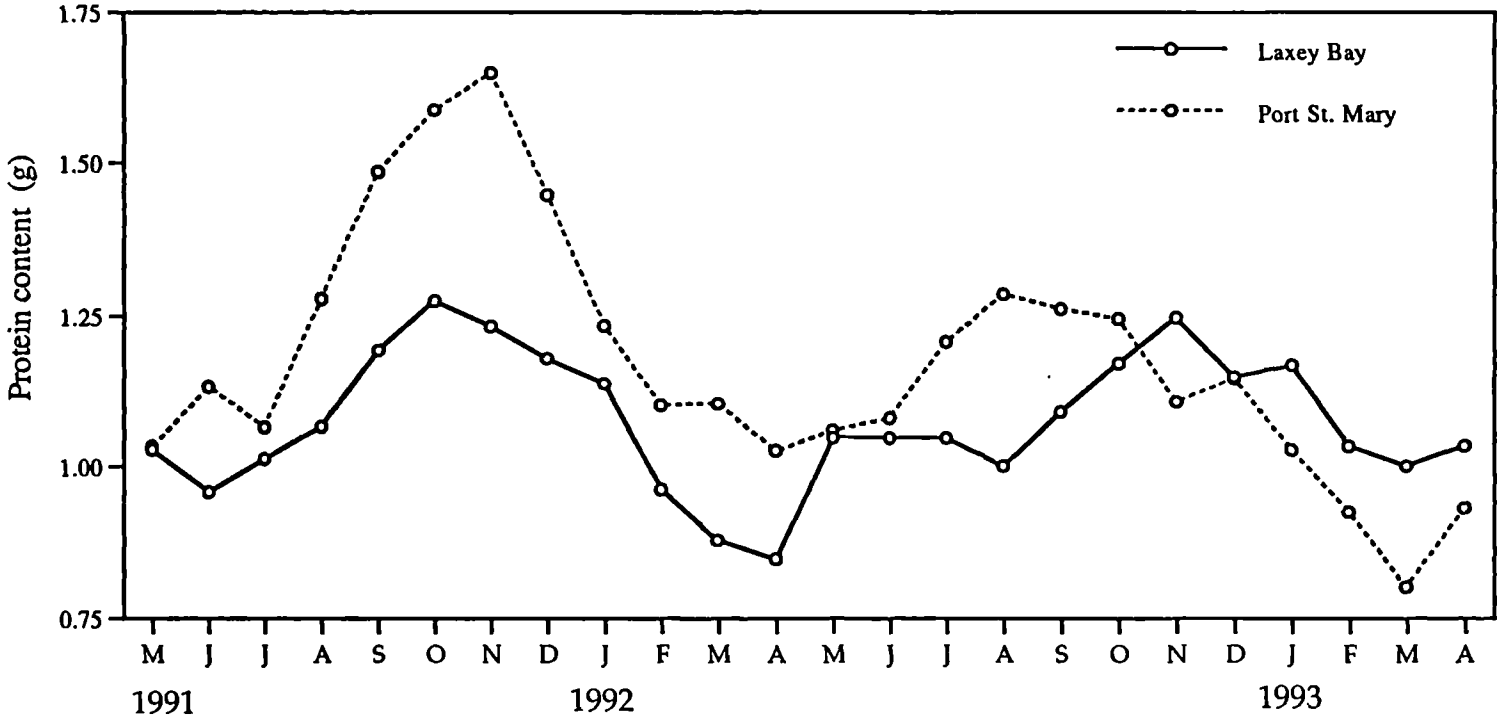


Fig.3.2b. Seasonal variation in the mean protein content of the adductor muscle of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St.Mary (n = 10 - 15).

the adductor muscle was very similar to that of the dry weight. The marked difference in the pattern of change between the percentage protein composition and the actual protein content must result from seasonal changes in other biochemical components.

b. Lipid

The percentage of lipid in the muscle remained low at only 3%- 4% for the whole study period (Fig. 3.3a) and showed no clear seasonal changes for the two populations, though some of the monthly values were significantly higher ($p < 0.05$) for the Laxey Bay population than for the Port St. Mary population (eg. January, February 1992 and February, March 1993).

The weight of lipid in the average adductor muscle was low (0.03 - 0.09 g) throughout the two years (Fig.3.3b) and followed a seasonal pattern of change on the two grounds which was very similar in relative amplitude and timing to the changes in protein content (Fig. 3.2b).

c. Glycogen

The adductor muscle glycogen showed the largest seasonal fluctuations of all the biochemical constituents observed (Figs. 3.4a and 3.4b). The percentage of glycogen ranged from 1% - 14% and 4% - 16% for *A. opercularis* from the Laxey Bay and Port St. Mary grounds respectively (Fig. 3.4a). An increase was observed in the percentage of glycogen throughout the spring and the summer, and reached a maximum in October and November for both populations in both years. The levels then decreased during the late autumn and winter, with the lowest values observed in March and April. The levels of glycogen were significantly

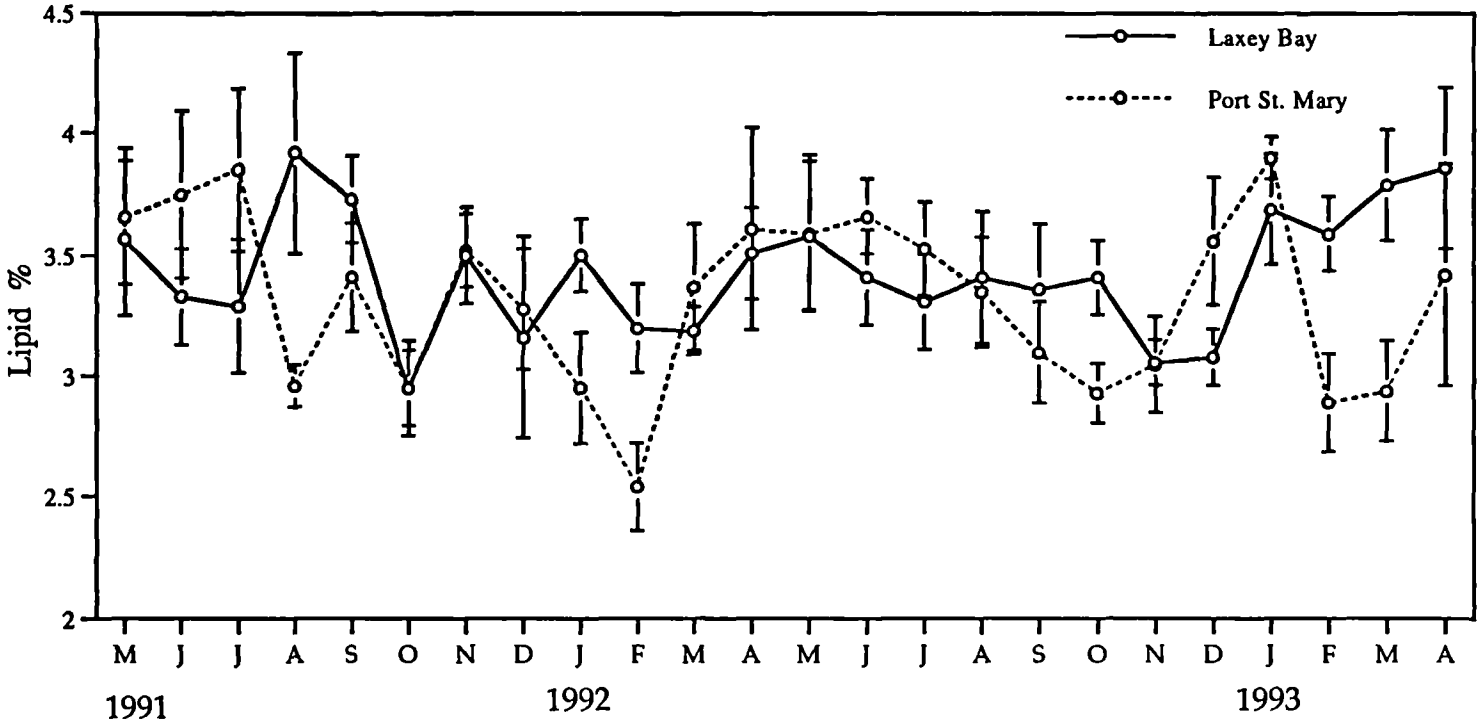


Fig 3.3a. Seasonal variation in the percentage lipid in the adductor muscle of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals (n = 10 - 15).

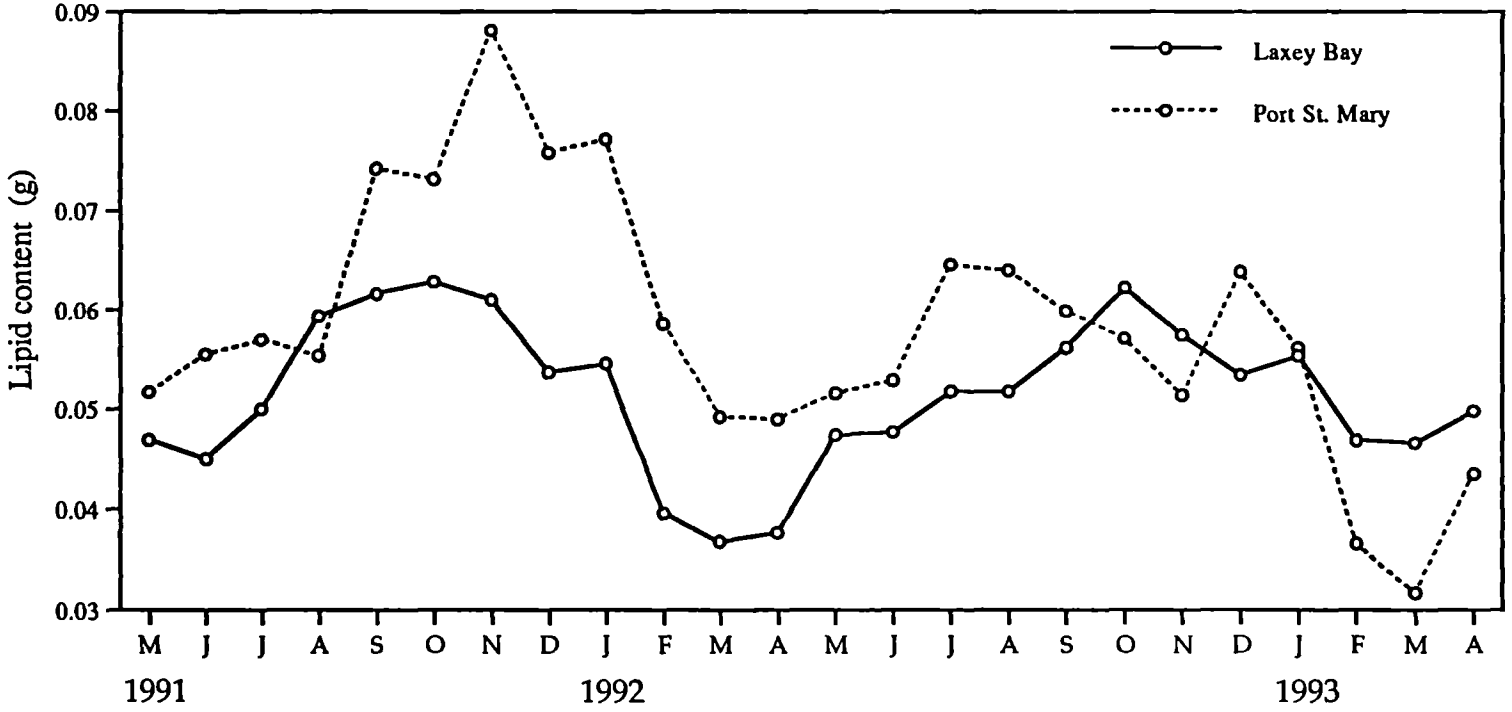


Fig. 3.3b. Seasonal variation in the lipid content of the adductor muscle of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St.Mary (n = 10 - 15).

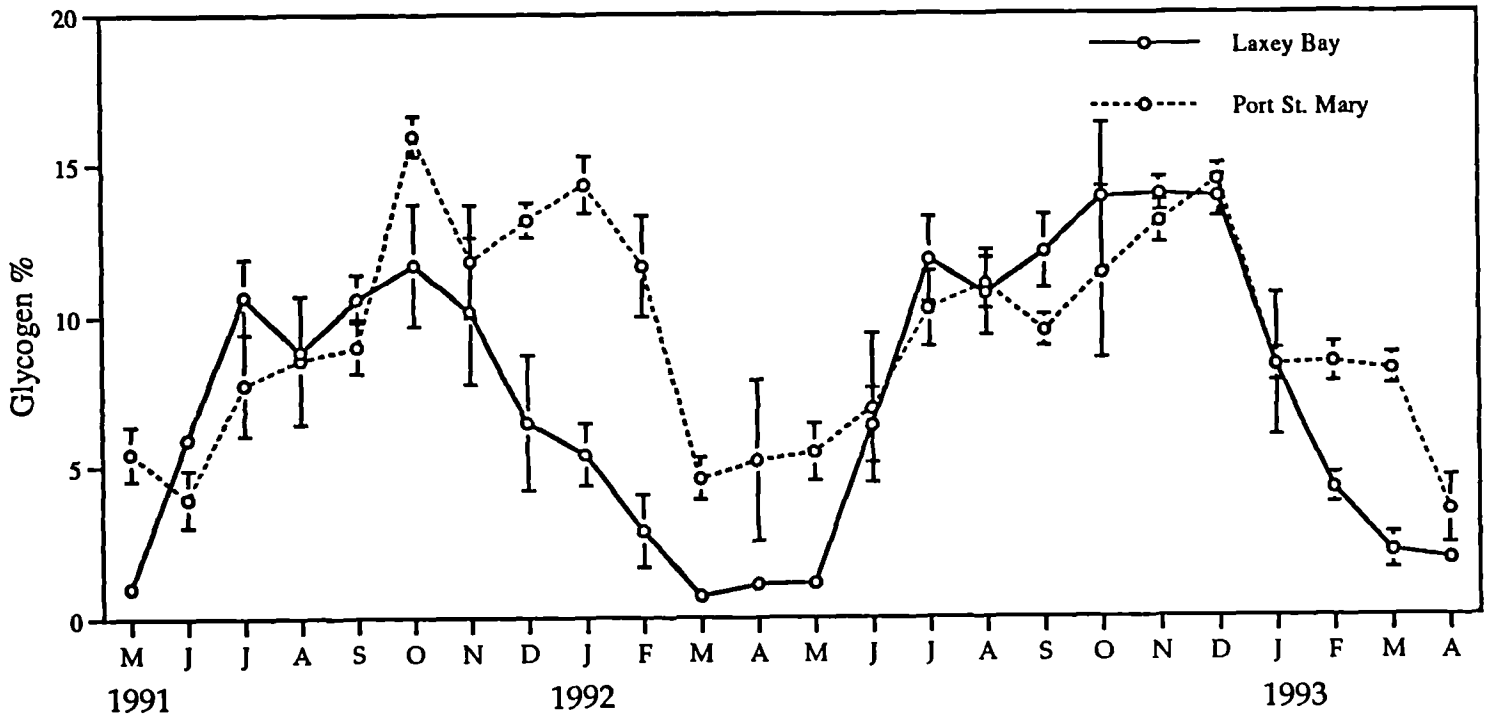


Fig. 3.4a. Seasonal variation in the percentage glycogen of the adductor muscle of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

higher ($p < 0.05$) in animals from the Port St. Mary ground, compared with Laxey Bay, in the periods December 1991 to March 1992 and February to April 1993.

The glycogen content of the average adductor muscle (Fig. 3.4b) showed a direct relationship to the dry weight of the muscle (Fig. 2.1). The glycogen content of animals from Laxey Bay rose to a maximum (0.21g) in October 1991 and was lowest in March 1992 (0.01g). The weight increased again from May to November 1992 (0.27g), then fell again to its lowest level in January 1993 (0.04g). The glycogen content of the population from the Port St. Mary ground rose to a much higher value during the first year, reaching a maximum in October 1991 (0.4g) before falling to a minimum level in March and April 1992 (0.07g). Throughout the second year the variation of glycogen content was similar to that of the Laxey Bay population. It was very clear that the *A. opercularis* from the Port St. Mary ground had a much higher glycogen content throughout most of the first year of sampling.

d. Ash.

During the period of two years, the ash weights of the adductor muscle of *A. opercularis* for both sampling areas increased in the spring and summer to reach a maximum in autumn; they then decreased over the winter to the lowest values in early spring (Fig. 3.5). The cycles were similar on the two grounds, though there was an indication that ash weight started to decline earlier on the offshore Port St. Mary grounds, in both years. Ash weights were also generally higher in animals from the Port St. Mary ground than Laxey Bay for most of the period of study, though only a few of the monthly values for the two grounds were significantly different ($p < 0.05$).

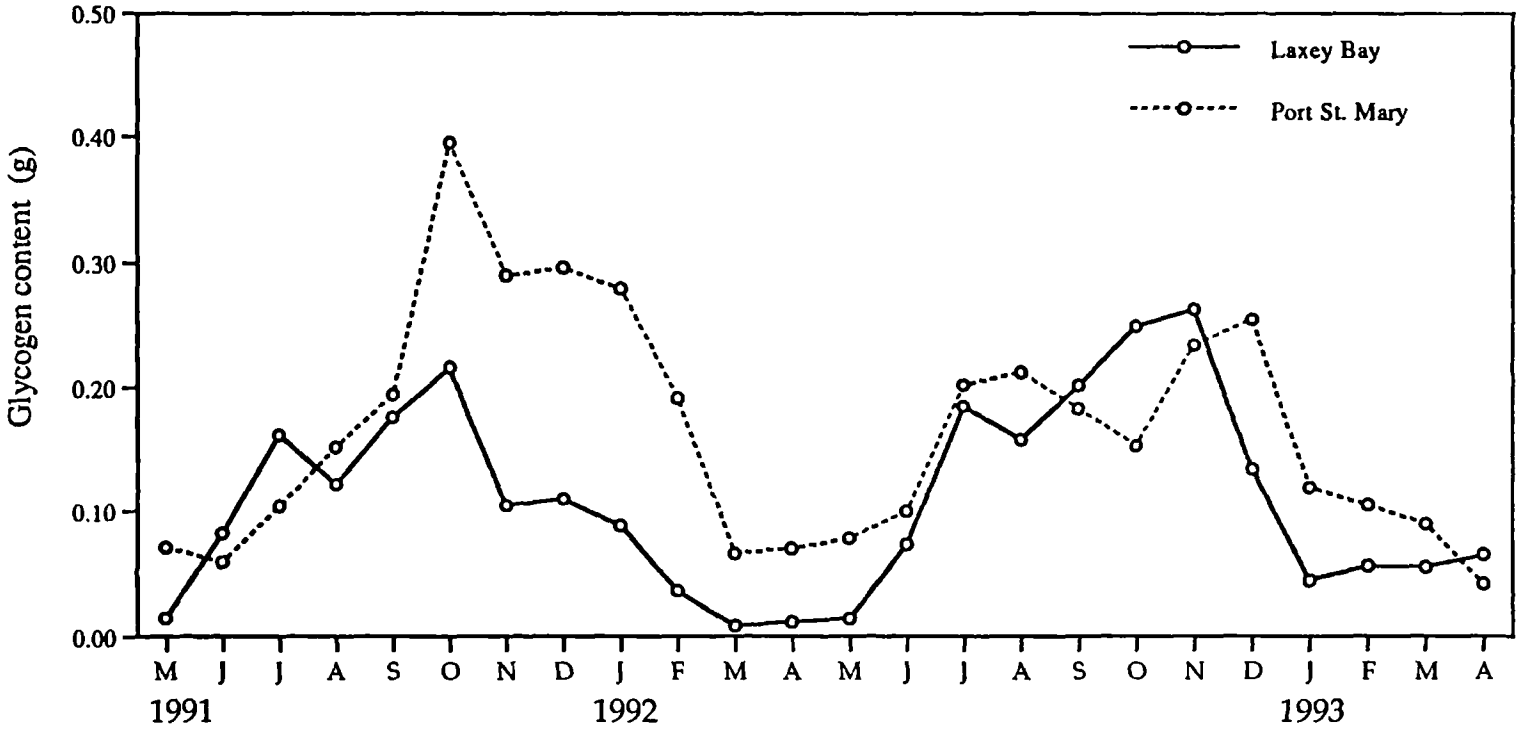


Fig. 3.4b. Seasonal variation in the glycogen content of the adductor muscle of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary (n = 10 - 15).

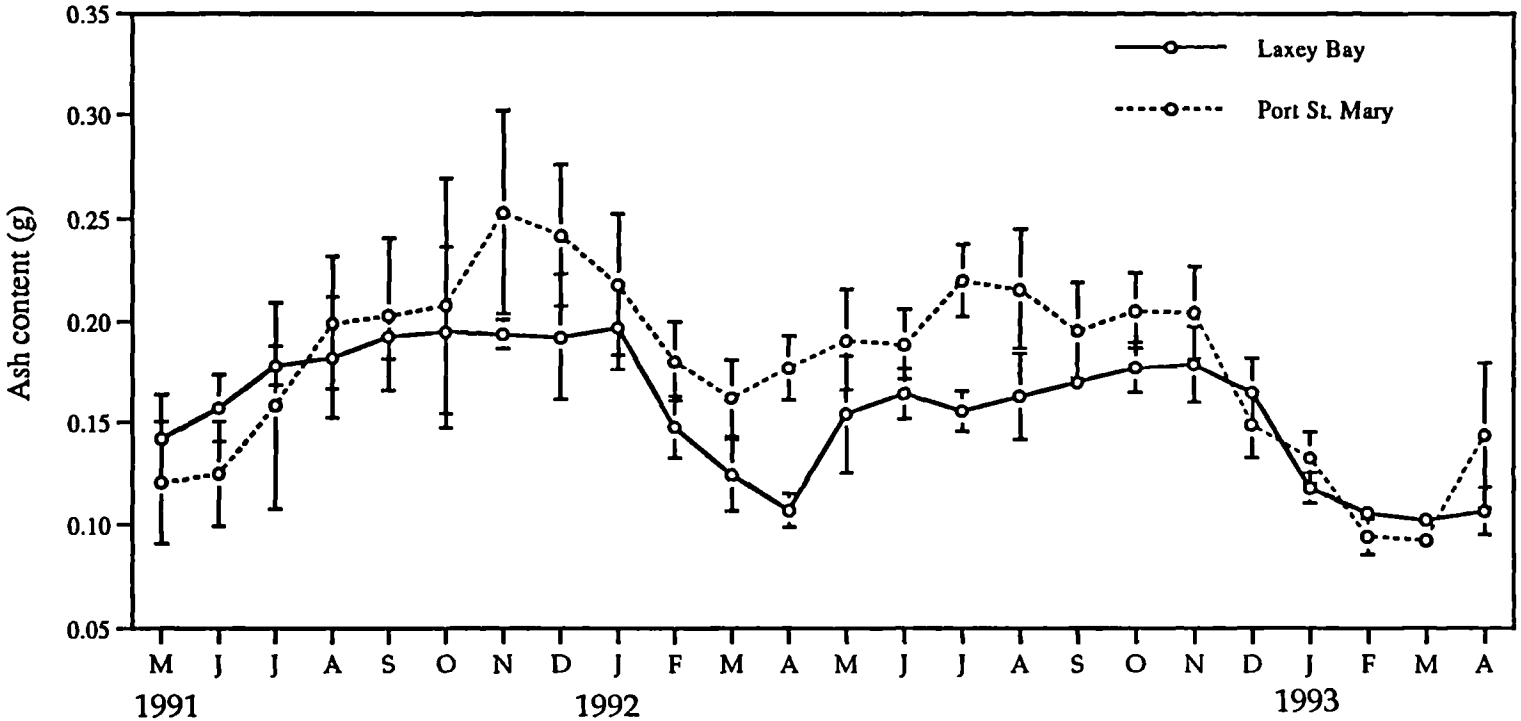


Fig. 3.5. Seasonal variation in the adductor muscle ash weight of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals.

The percentage of ash also followed a similar pattern to the content, ranging from 7% - 12% and 7% - 13% for the Laxey Bay and Port St. Mary grounds respectively.

e. Water

The percentage water content of the adductor muscle varied during the year for both populations. It reached a maximum level in late winter or early spring, while the lowest level was noted in autumn (Fig. 3.6). *A. opercularis* from Laxey Bay exhibited their minimum percentage of water in October 1991 (75.86%) and November 1992 (75.05%), while maximum values were recorded in April 1992 (79.92%) and in March 1993 (79.15%). A similar variation was observed in the Port St. Mary samples, the lowest values being in November 1991 (73.55%) and October 1992 (74.96%) and the highest in April 1992 (78.66%) and March (1993 (79.63%). During the period November 1991 to April 1992, the water content of the adductor muscle from the Port St. Mary ground was significantly lower ($p < 0.05$) than the Laxey Bay samples (Fig. 3.6) but this position was reversed in May 1991 and again in May and June 1992. For the rest of the study period there was no significant difference between the two grounds.

The range of values recorded agree closely with those obtained by Soemodihardjo (1974) for the north Irish Sea (76-86%) and for a population in the Clyde Sea (74-83%) (Taylor & Venn, 1979). The percentage water content followed an inverse relationship with the variation of adductor muscle dry weight.

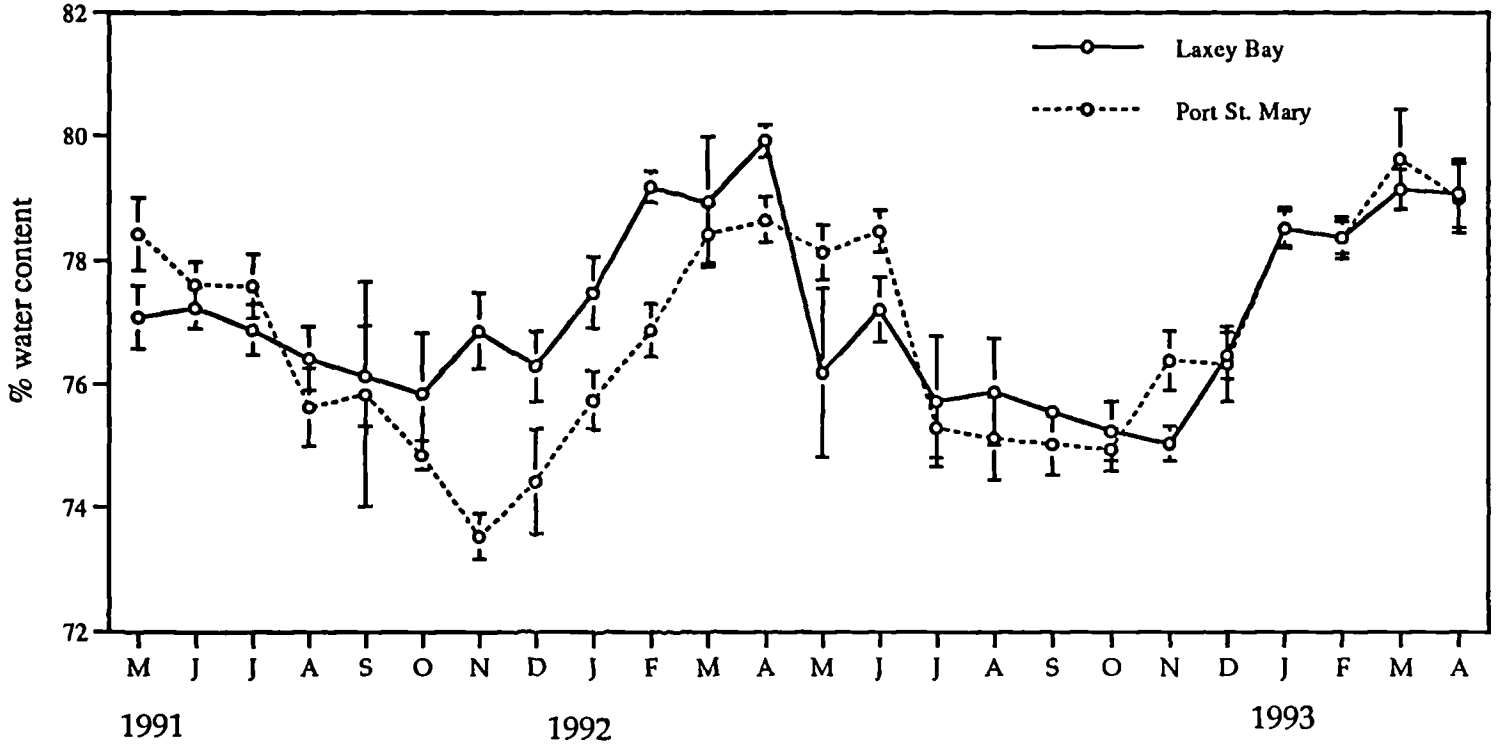


Fig. 3.6. Seasonal variation in the percentage water content of the adductor muscle of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals.

3.3.1.2 Gonad (testis and ovary)

Protein, lipid and glycogen were analysed separately in the testis and the ovary to observe their biochemical differences during gametogenesis. The percentage composition for separate organs and the combined biochemical contents (for testis and ovary together) are shown in the figures.

a. Protein

The percentage of protein in the testis increased with the development of the gonads during the winter and through spring prior to spawning (Fig. 3.7). The protein levels immediately decreased in both populations when they spawned. The lowest levels of protein were observed during the autumn, especially the months of October and November. Protein levels ranged from 52% - 70% and 53% - 74% for the animals from the Laxey Bay and Port St.Mary ground respectively. Some of the paired monthly values were statistically significantly ($p<0.05$) different between the two populations but there was no obvious pattern.

The percentage protein in the ovary showed lower levels, compared with the testis, ranging from 47% - 60% for the *A. opercularis* from Laxey Bay and 48% - 58% for the Port St. Mary ground (Fig. 3.8). The seasonal variation observed was similar to the variation of testis over the two years but percentage protein values in the ovaries were generally higher ($p <0.05$) in the summer and early autumn in the Laxey Bay population, compared with Port St. Mary.

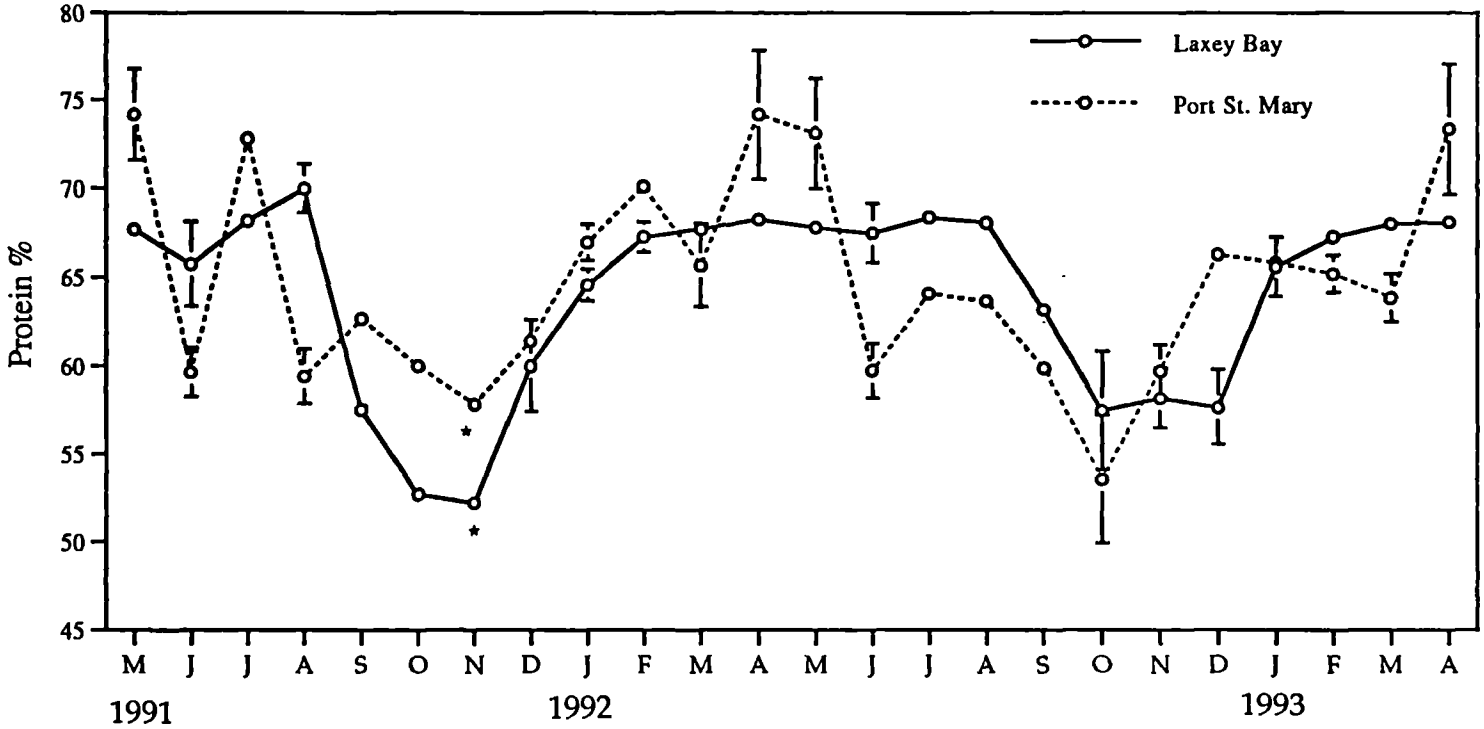


Fig. 3.7. Seasonal variation in the percentage composition of protein in the testis of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (* pooled data).

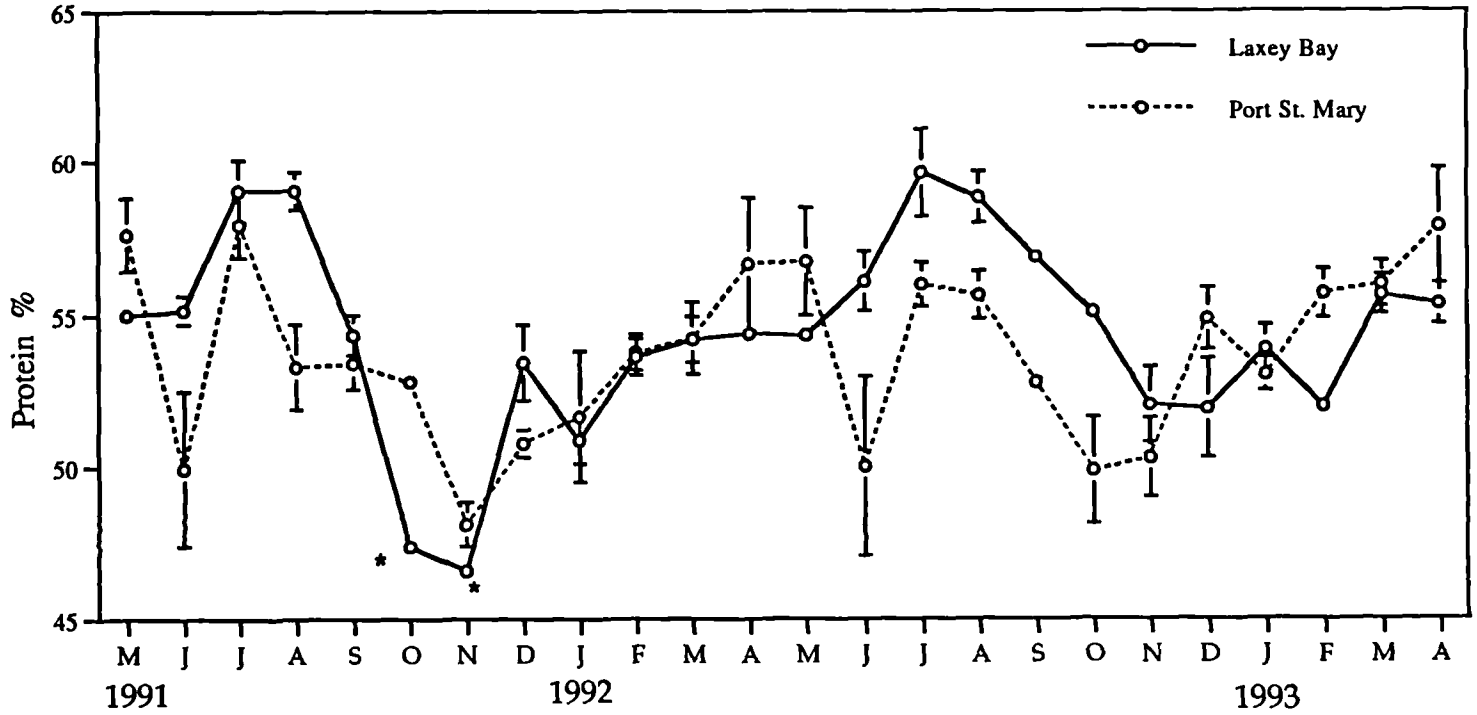


Fig. 3.8. Seasonal variation in the percentage composition of protein in the ovary of *Aequipecten opercularis* (60 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (* pooled data).

b. Lipid

The percentage of lipid in the testis remained low throughout the study and showed no clear seasonal changes (Fig. 3.9). This ranged from 3% - 7% and 3% - 8% for the populations from Laxey Bay and the Port St.Mary ground respectively. However, some of the paired monthly values were significantly different ($p < 0.05$) between the two grounds, particularly in the summer months, and this probably reflects differences in the timing of spawning peaks on the two grounds.

In contrast to the testis, the lipid of the ovary showed a clear seasonal variation (Fig. 3. 10). Lipid levels increased during gonad development and decreased with the release of gametes. Significant drops in lipid levels between consecutive months (eg. May - June 1992 and January - February 1993 on the Port St. Mary ground) suggest that partial spawnings have occurred. The percentage of lipid increased in animals from both grounds during the late autumn and reached its maximum level in spring (March - April). In both years the increase occurred 1-2 months earlier on the Port St. Mary ground. The lowest values were recorded in September and October in 1991 and in 1992 respectively. The lipid levels of *A. opercularis* from Laxey Bay and Port St. Mary varied from 5% - 24% and 6% - 20% over the period of the study. The values recorded were generally significantly higher ($p < 0.05$) for the Laxey Bay population in April, May and June and for the Port St. Mary population in December and January, in both years of study.

c. Glycogen

The percentage of glycogen for both testis and ovary remained relatively low compared with the adductor muscle but the seasonal cycle was readily

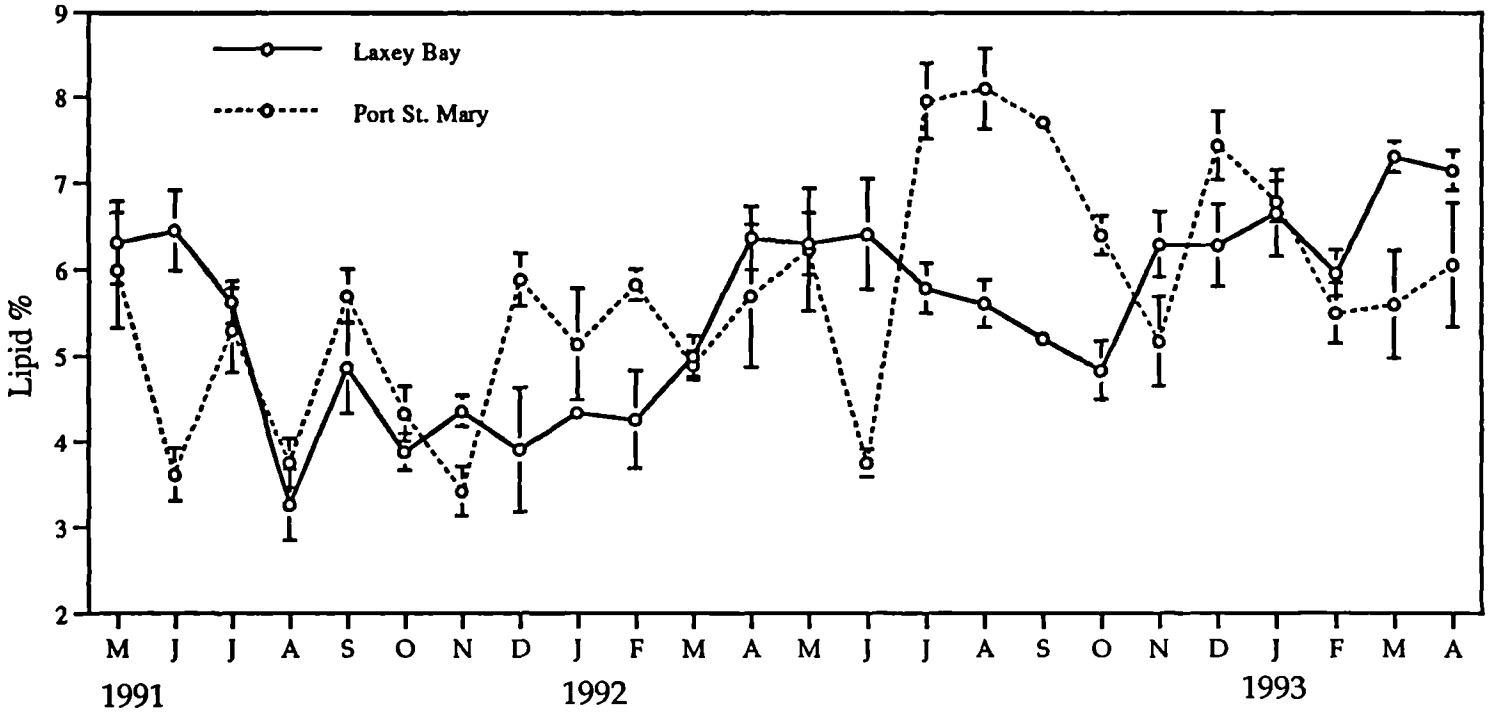


Fig. 3.9. Seasonal variation in the percentage composition of lipid in the testis of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph.

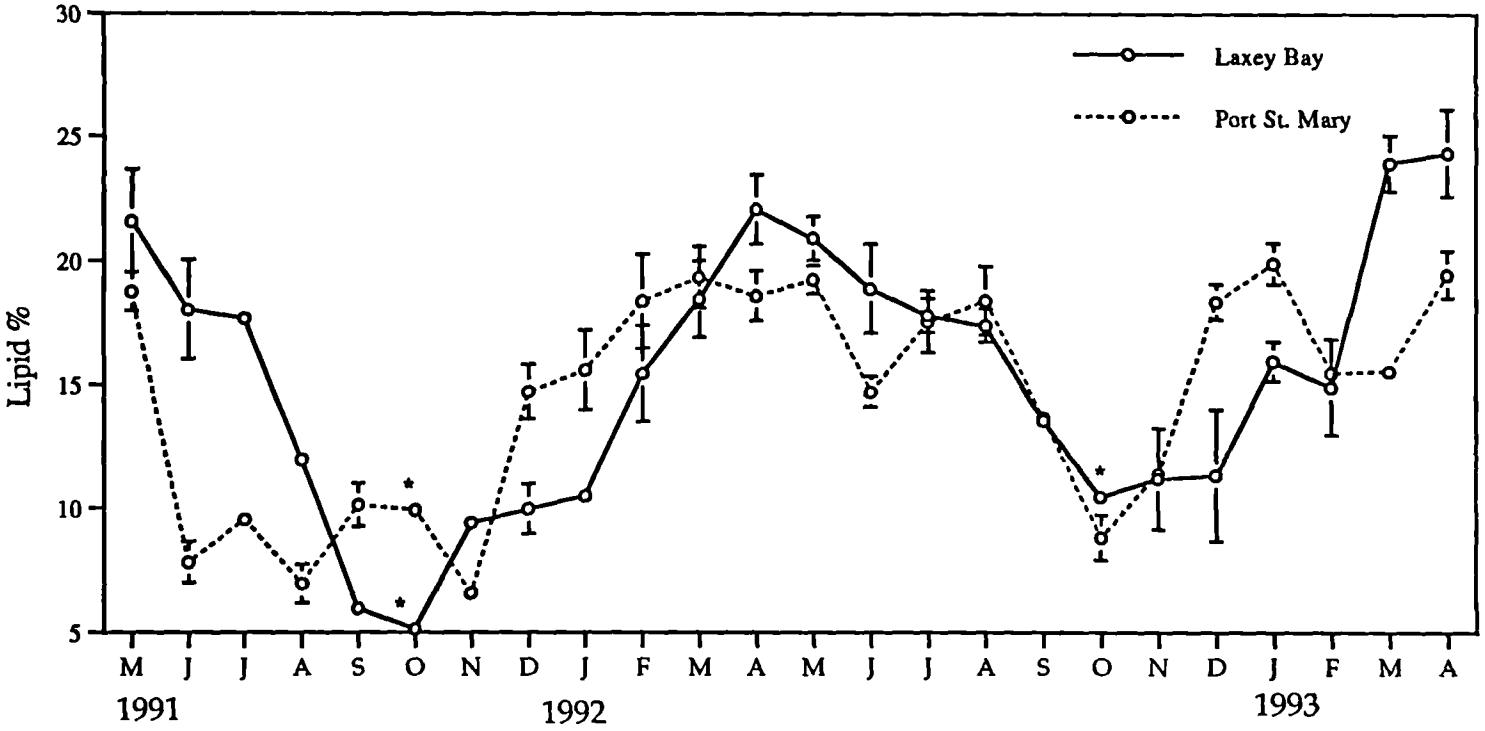


Fig. 3.10. Seasonal variation in the percentage composition of lipid in the ovary of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (* pooled data).

apparent in both gonad portions (Fig. 3.11 and Fig. 3. 12). The glycogen level of the testis (Fig. 3.11) ranged from 2% - 7% for Laxey Bay and from 2% - 8% for the Port St. Mary ground during the period observed. Glycogen levels in the testis fell during the summer to a low level in autumn, then increased through the winter. This increase occurred earlier and more rapidly on the Port St. Mary ground and the subsequent decline was more variable. This reflects differences in the cycles of gametogenesis and spawning on the two grounds and resulted in statistically significant ($p < 0.05$) differences between the paired values for much of the year.

The percentage of glycogen in the ovary (Fig. 3.12) was also low ranging from 2% - 7% over the same period. Significant differences between the levels of glycogen in the ovaries for the Laxey Bay and Port St. Mary populations showed a similar pattern to the testis. The lowest glycogen values were recorded during the autumn and values were highest during gametogenesis in winter and immediately prior to spawning. As with the testis, the increase in percentage glycogen occurred earlier and more rapidly in the offshore Port St. Mary population.

d. Absolute biochemical composition

Fig. 3.13 shows the total biochemical contents of protein, lipid and glycogen in the gonad (testis and ovary combined) during the study period for the two grounds. The contents followed a similar seasonal pattern to the gonad dry weights in the two populations (Fig.1.8). During gametogenesis, and prior to spawning, contents values were highest and then decreased immediately after spawning. Differences in the biochemical contents of the Laxey Bay and Port St. Mary populations over the same period indicate the pattern of gametogenesis and spawning differed at each grounds with an

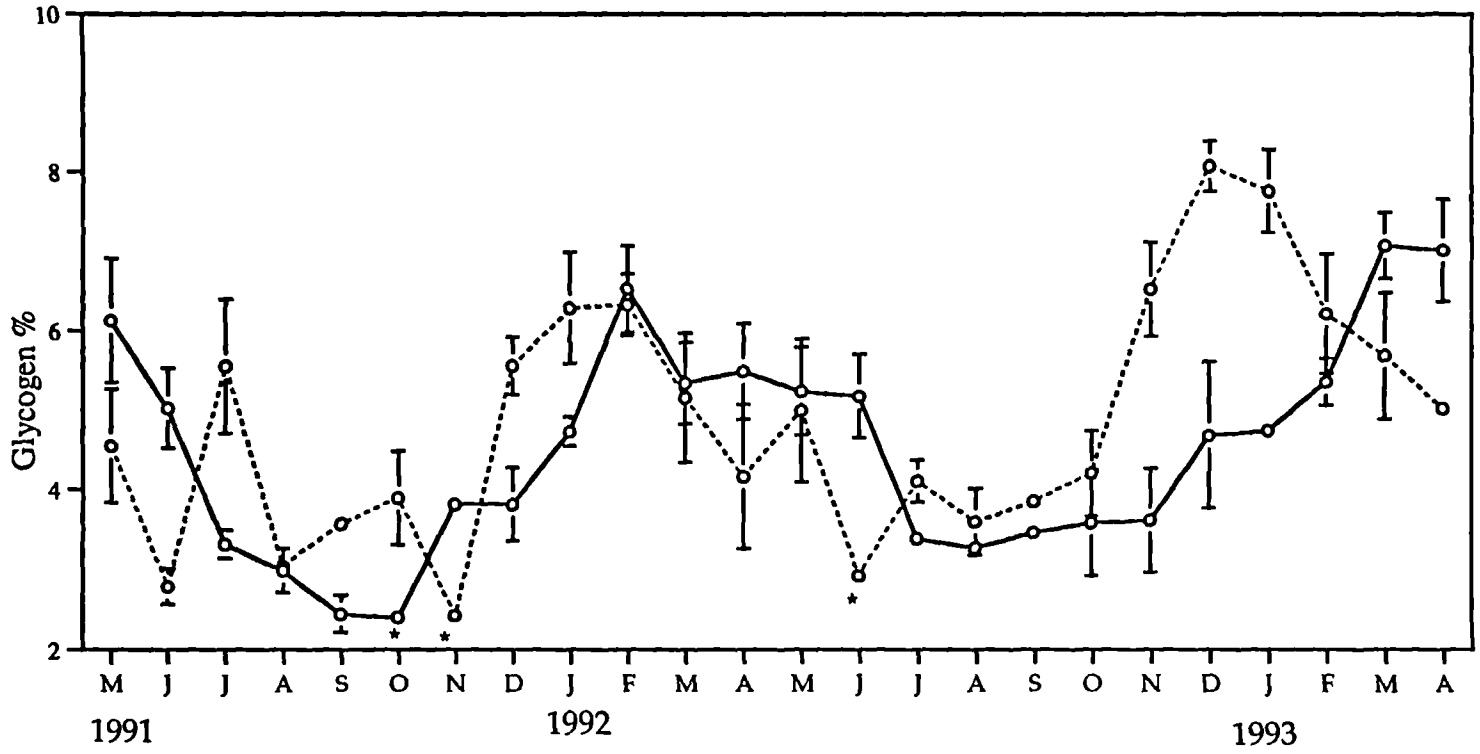


Fig. 3.11. Seasonal variation in the percentage composition of glycogen in the testis of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay the Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (* pooled data).

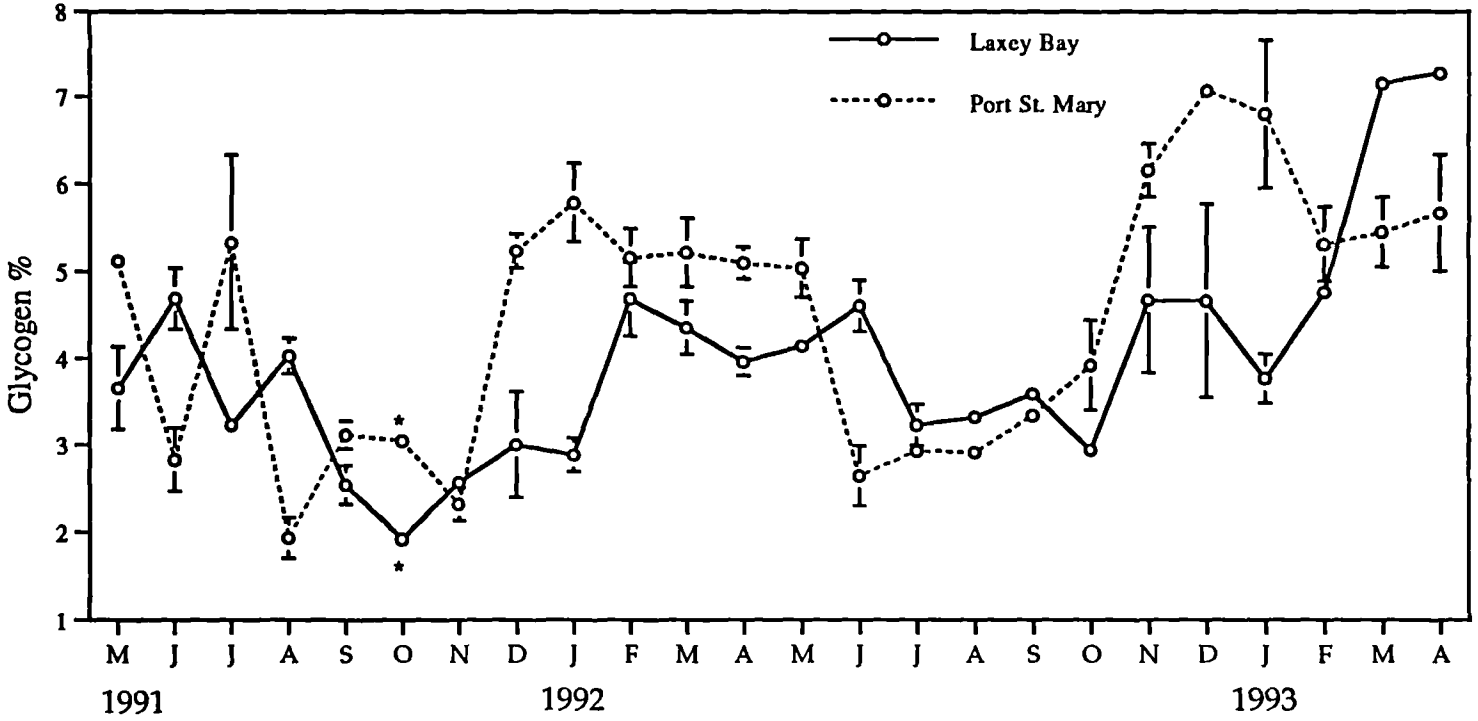


Fig. 3.12. Seasonal variation in the percentage composition of glycogen in the ovary of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (* pooled data) (n = 10 - 15).

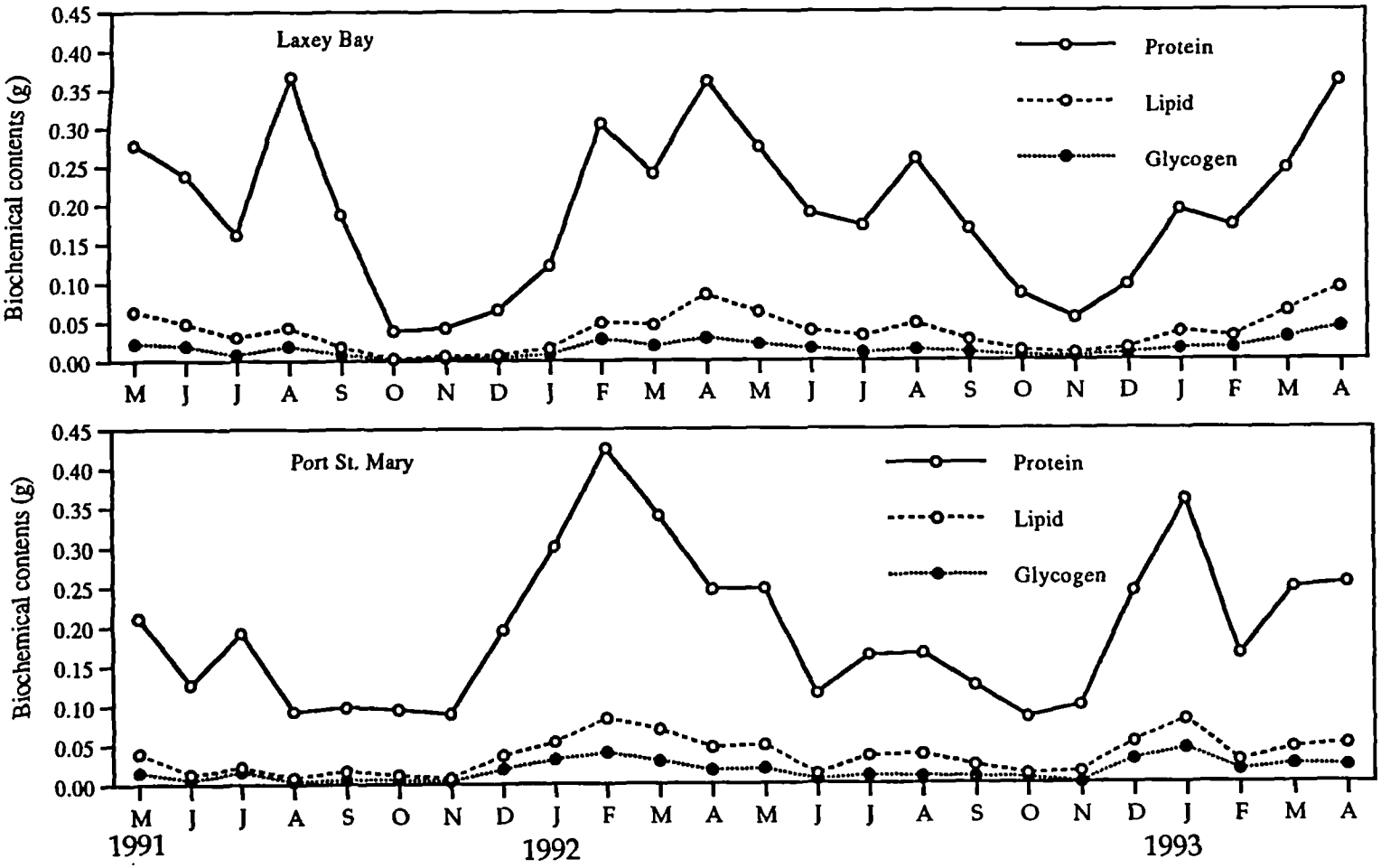


Fig. 3.13. Seasonal variation in the protein, lipid and glycogen content of gonad (testis and ovary combined) of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary (n = 10 - 15).

earlier and more rapid build-up of the gonads at Port St. Mary, and no indication of an autumn spawning at this ground.

e. Ash

The percentage of ash varied between 10% and 22% for both populations over the two year sampling period.

The weight of ash for the average weight gonad (Fig. 3.14) was directly related to the size of the gonad. The minimum ash weight was noted during the early autumn for both populations. The weight gradually increased during the winter and reached its highest immediately before spawning. During the period of gonad development (winter) the ash weight of animals from the Port. St. Mary ground showed significantly ($p < 0.05$) higher values than the animals from Laxey Bay, particular during 1991/92 when they were much higher than in 1992/93.

f. Water

The water content of scallop gonads is at a minimum when the gonads are fully developed and increases during the spawning period due to the admission of water into the gonad after the release of the gametes to the environment (Soemodihardjo, 1974; Sastry, 1976; Taylor and Venn, 1979). This situation was clearly observed in both populations over the experimental period (Fig. 3.15). The percentage water content of samples from Laxey Bay was lowest in August 1991 (76.25%), in February (77.22%) and March 1992 (76.59%) and in April 1993 (77.32%). The highest percentage water content was in October 1991 (87.71%) and in November 1992 (89.45%). The *A. opercularis* from the Port St. Mary ground had their

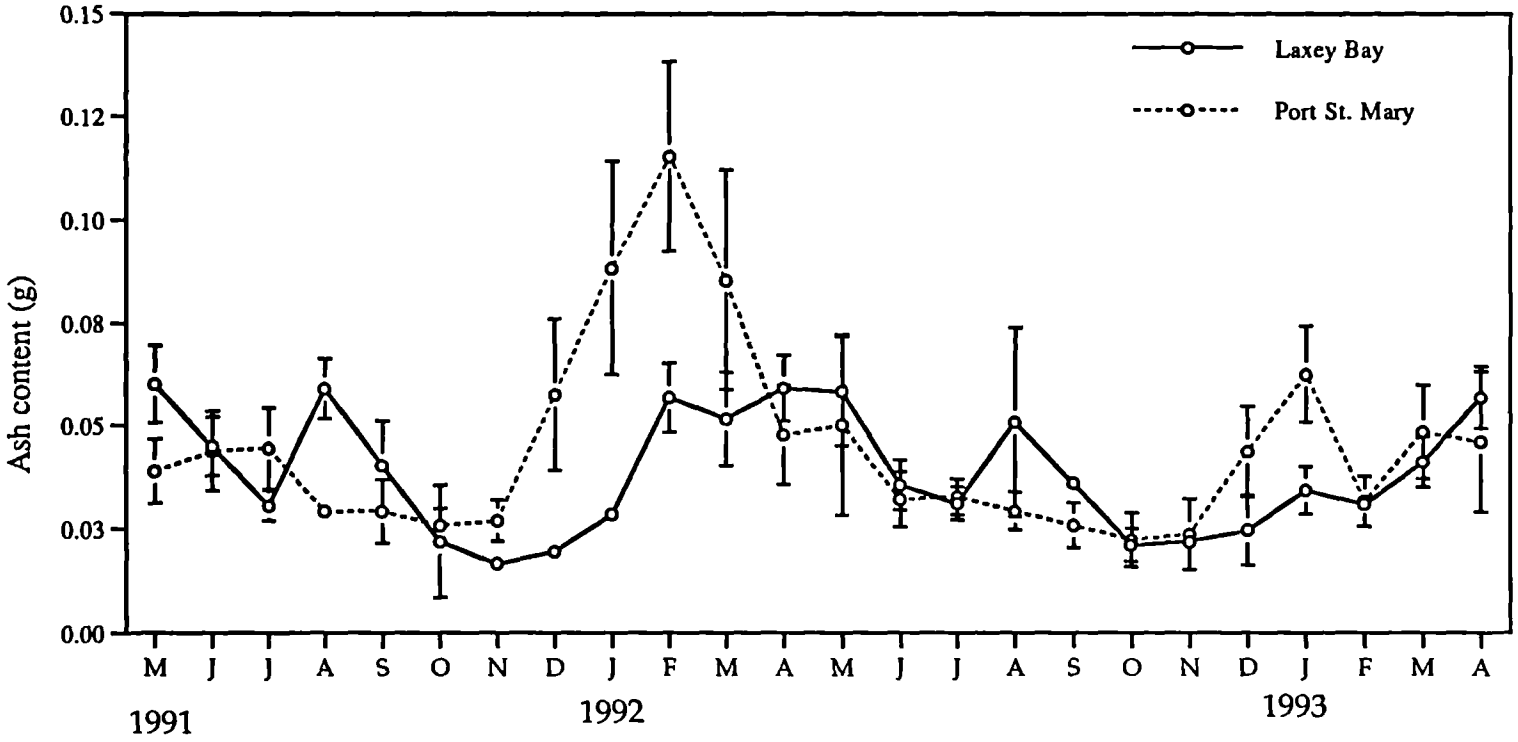


Fig. 3.14. Seasonal variation in the gonad ash content of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph.

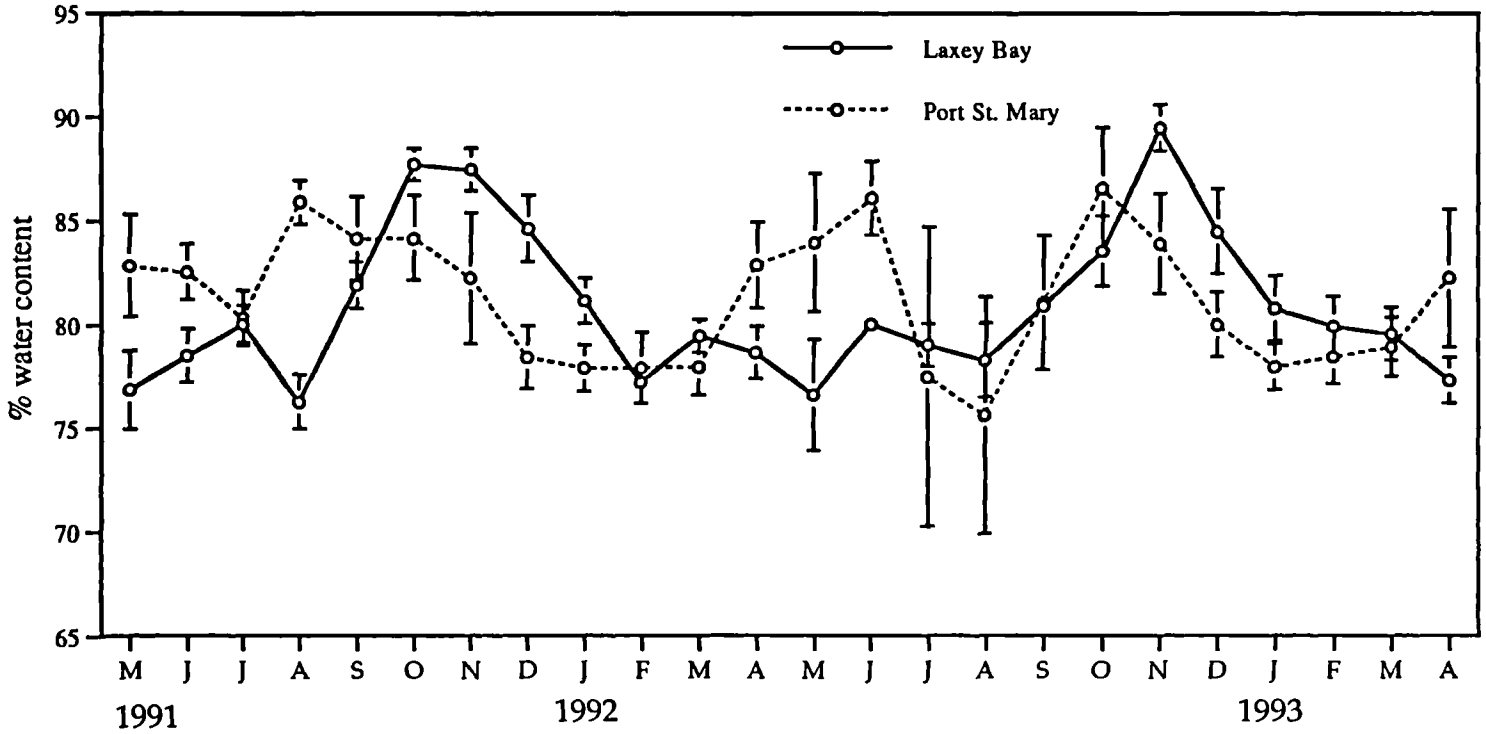


Fig. 3.15. Seasonal variation in the percentage water content of the gonad (testis and ovary) of *Aequipecten opercularis* (60 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph.

lowest water contents in June 1991 (80.33%), between January and March (77.92%) and again in August 1992 (75.63%), and in January 1993 (77.98%). At the same ground the percentage water content was highest in August 1991 (85.89%) and in June (86.09%) and October 1992 (86.56%). The seasonal cycles at the two grounds were therefore out of phase being some 1-2 months earlier and with an additional peak in late spring/early summer at the Port St. Mary ground. In consequence, the values recorded at the two grounds were significantly different ($p < 0.05$) for most months of the year.

3.3.1.3 Mantle tissue

a. Protein

Protein forms a large percentage of the mantle tissue. The percentage of protein varied from 59% - 66% and 59% - 71% for the animals from Laxey Bay and Port St. Mary respectively. An increase in the percentage protein was observed during the winter and spring for both populations in both years (Fig. 3.16a). However, this rise occurred 1-2 months earlier in animals from Port St. Mary in 1991/92 and reached a much higher maximum than for the Laxey Bay population. As a result the level of protein was significantly higher ($p < 0.05$) in *A. opercularis* from the offshore ground in the period January to May 1992, as it was in May-July 1991 and April 1993. For the rest of the period of study the protein levels fluctuated similarly in both populations.

The actual weight of protein present in mantle tissue increased during the summer and reached its maximum in autumn (Fig. 3.16b). During the late autumn and winter the weight decreased and reached its lowest level in early spring. The content of protein rose to a much higher level in the

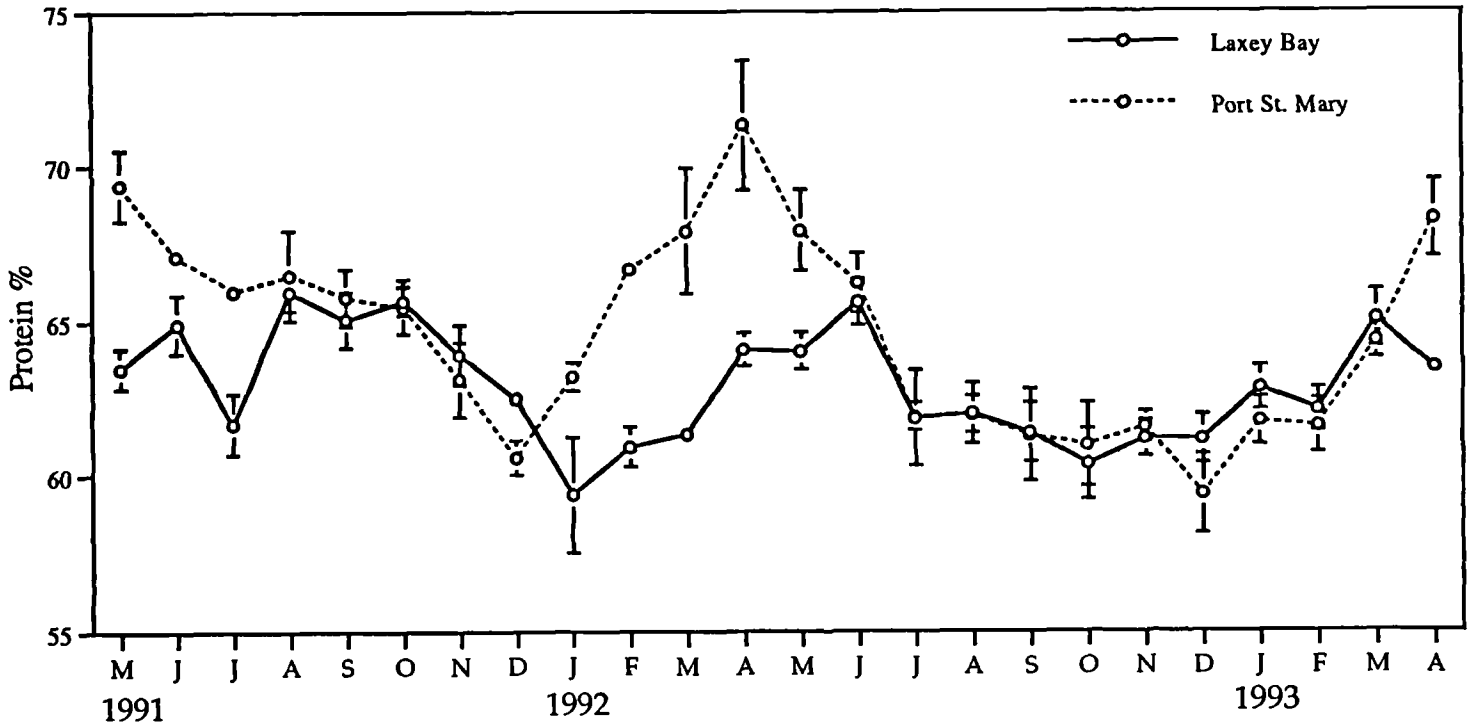


Fig. 3.16a. Seasonal variation in the percentage composition of protein in the mantle tissue of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

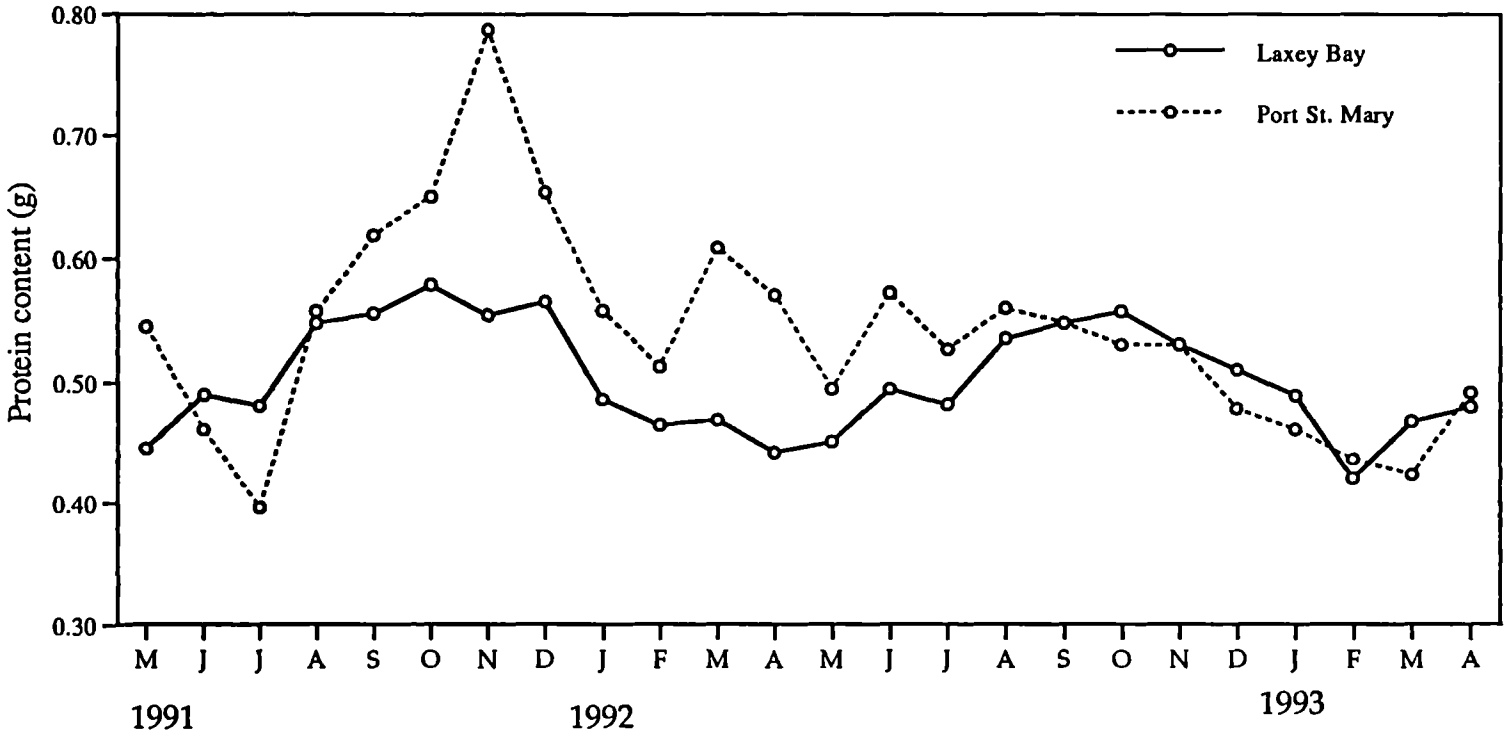


Fig. 3.16b. Seasonal variation in the protein content of mantle tissue of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary (n = 10 - 15).

mantle tissue of *A. opercularis* from the Port St. Mary ground in autumn 1991, than in Laxey Bay animals, or for both grounds in autumn 1992, and remained at a higher level than Laxey Bay until August 1992.

b. Lipid

The percentage of lipid in the mantle tissue was low at only 2% - 4% throughout the period of study but the monthly values were highly variable, as indicated by the high 95% confidence limits (Fig. 3.17a) and no clear seasonal cycles were apparent.

The mean absolute content of lipid in the mantle tissues also remained at a relatively constant and low level, ranging from 0.02g - 0.04g over the duration of two years. There was some indication of a seasonal variation (Fig. 3.17b) which followed the same pattern as the protein contents, rising to a higher level in autumn and decreasing in early spring.

c. Glycogen

The percentage composition and the absolute content of glycogen showed very well marked seasonal variations which were similar in pattern to the variations of dry weight of the tissues in both populations. For the Laxey Bay population there were two clear peaks in the percentage glycogen, in July and October 1991 and in July and November 1992, while for the Port St. Mary population there was only one peak which occurred in October in both years (Fig. 3.18a). In both sets of samples the lowest levels of glycogen occurred during the late winter and early spring. The level of glycogen was significantly higher ($p < 0.05$) in queenies from the Port St. Mary ground for most of the time throughout the observation period.

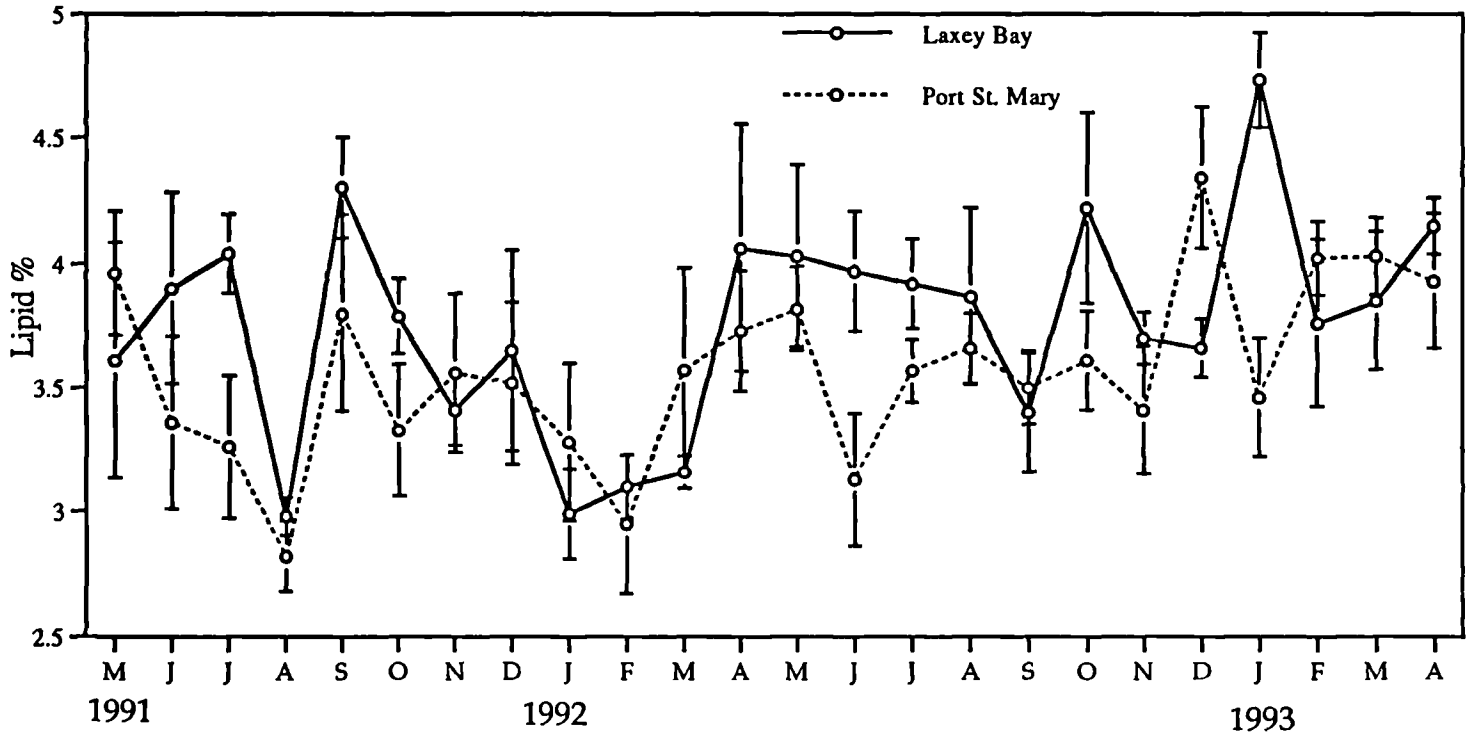


Fig. 3.17a. Seasonal variation in the percentage composition of lipid in the mantle tissue of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

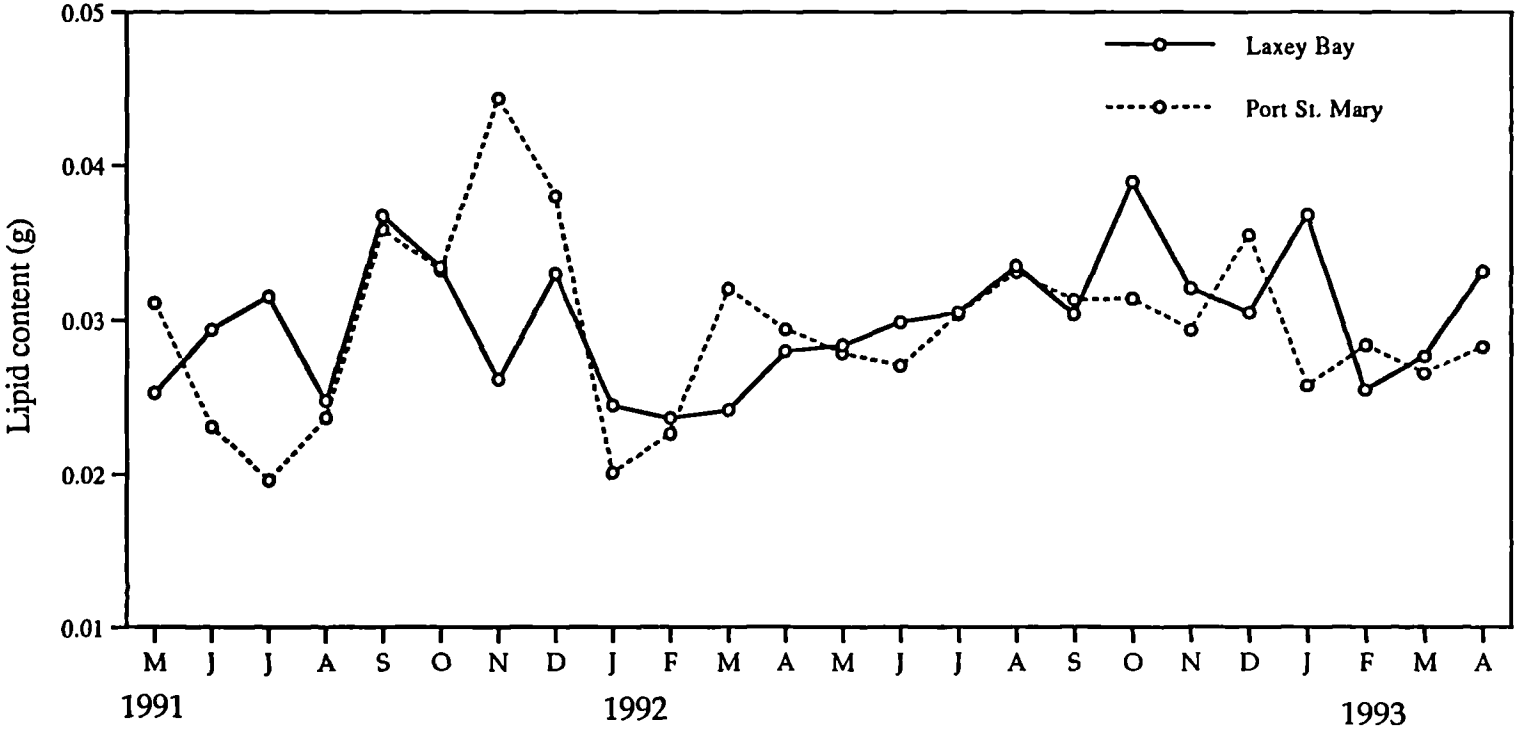


Fig. 3.17b. Seasonal variation in the lipid content of mantle tissue of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary (n = 10 - 15).

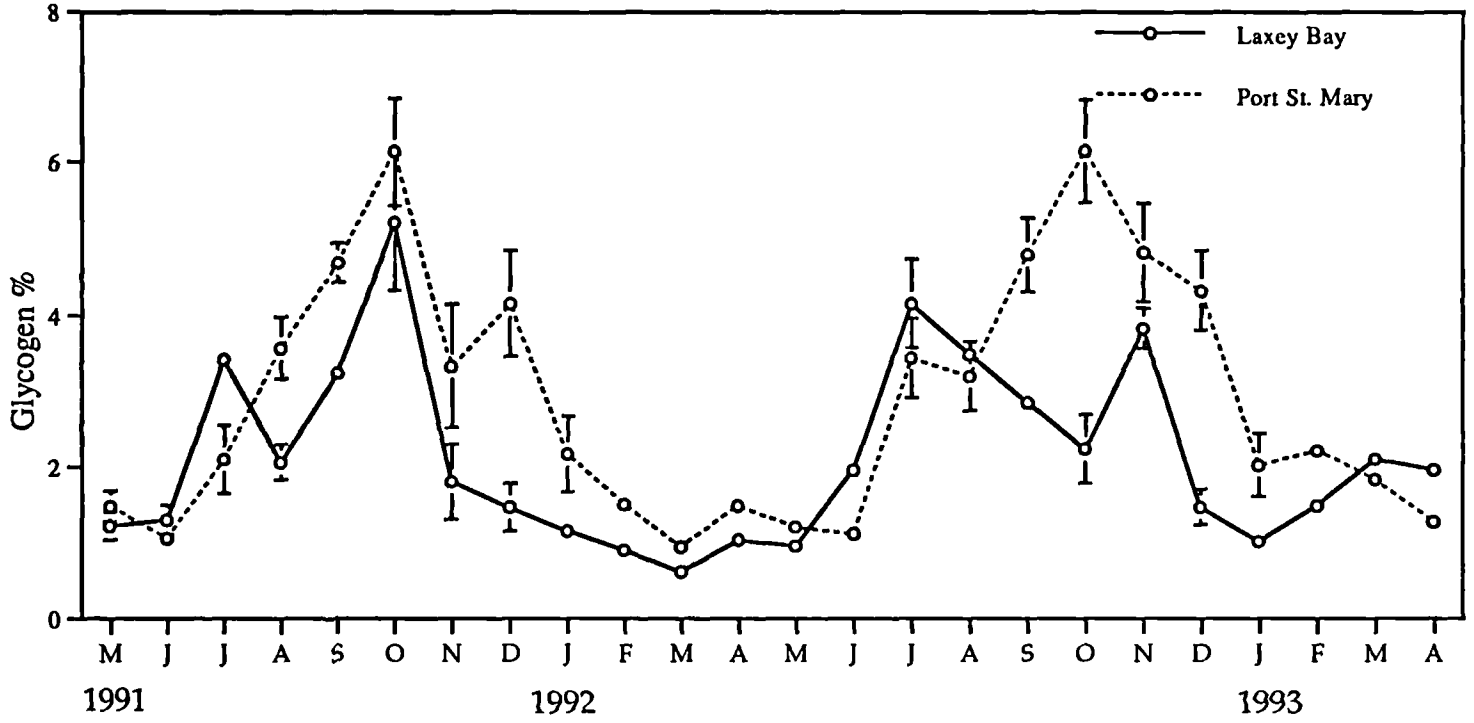


Fig. 3.18a. Seasonal variation in the percentage composition of glygogen in the mantle tissue of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

The absolute content of glycogen was very low and varied from 0.007g - 0.046g for the *A. opercularis* from Laxey Bay and 0.009g - 0.061g for animals from the Port St. Mary ground (Fig. 3.18b). The weight of glycogen remained higher for animals from the Port St. Mary ground, compared with Laxey Bay, throughout the year.

d. Water

The water content of the mantle tissue (Fig. 3.19) showed a similar seasonal variation to the adductor muscle water content (Fig. 3.6) but to a lesser degree. It is interesting to mention that, throughout the year, the water content of the mantle tissue was greater than that of the adductor muscle. The mantle tissue water content of the two populations varied from 85% - 90%, while adductor muscle water content changed from 75% - 80% throughout the period. The high water content of the mantle tissue reflects the fact that this tissue is an important part of the haemolymph circulatory system of bivalves molluscs (Brand, 1972) and contains a large volume of body fluid.

3.3.1.4 Digestive gland

a. Protein

The percentage composition and absolute content of protein in the digestive gland show clear seasonal variations for the two populations (Fig. 3.20a, b).

The percentage of protein (Fig. 3.20a) in the digestive gland increased during the early spring and reached its highest level in April - May for both

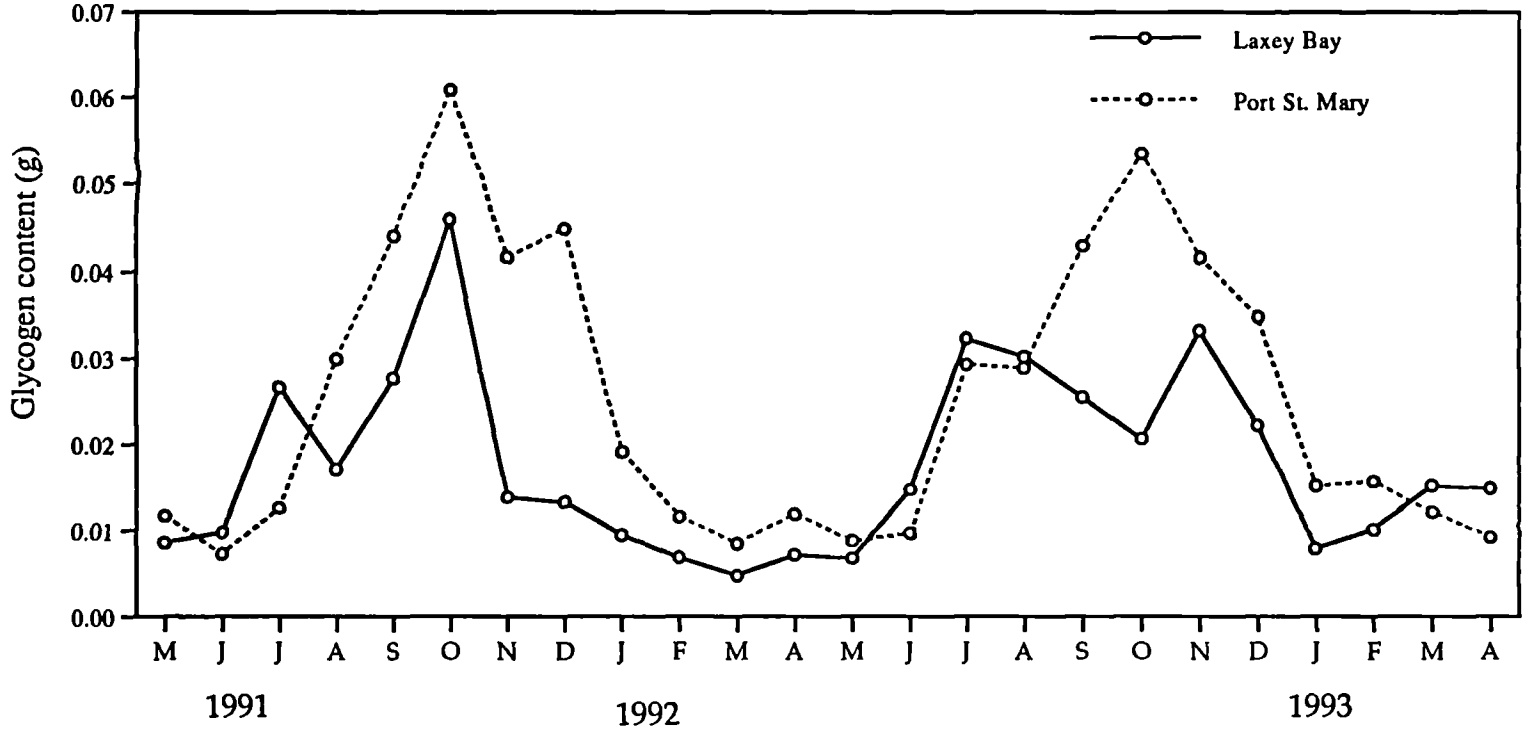


Fig. 3.18b. Seasonal variation in the glycogen content of mantle tissue of *Aequipecten opercularis* (65 - 70 mm shell length length) from Laxey Bay and Port St. Mary (n = 10 - 15).

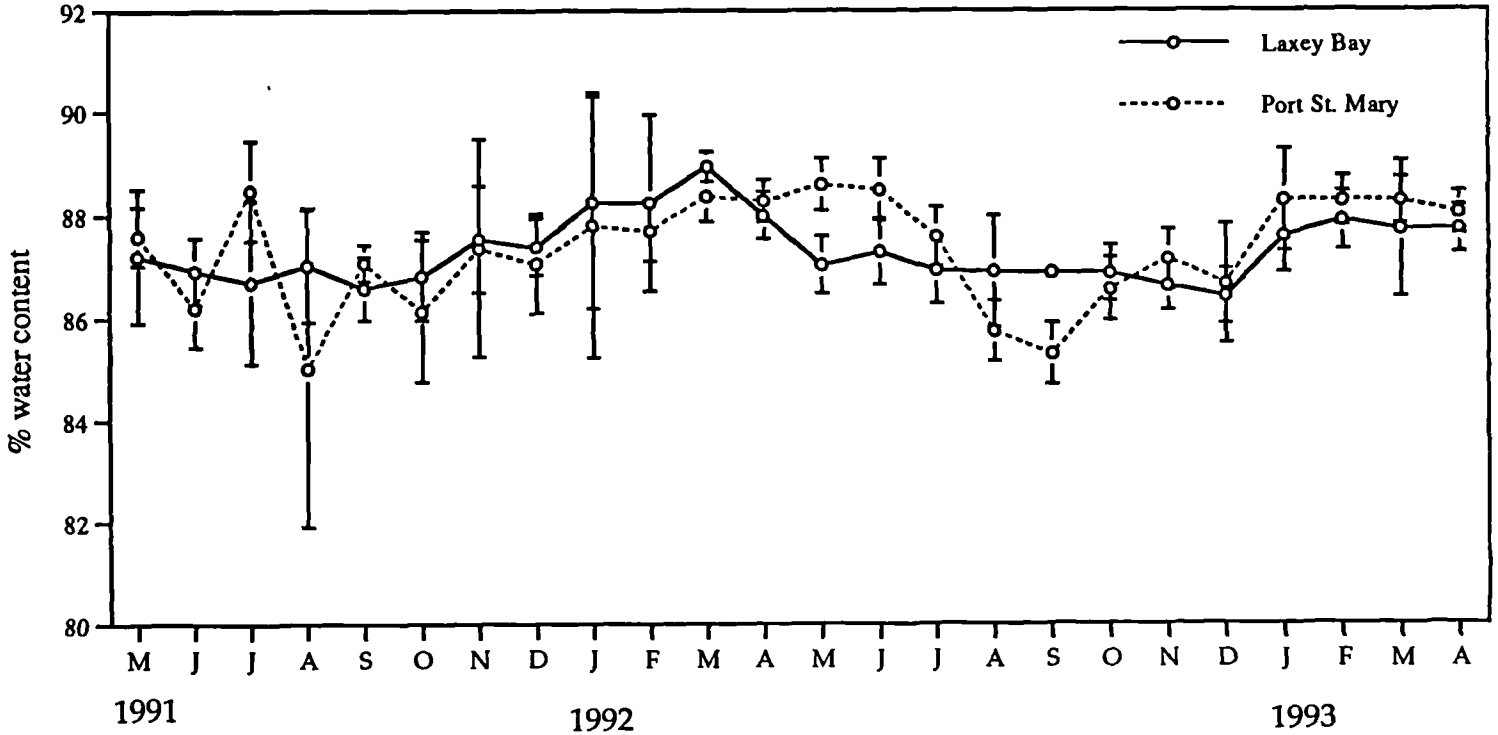


Fig. 3.19. Seasonal variation in the percentage water content in the mantle tissue of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

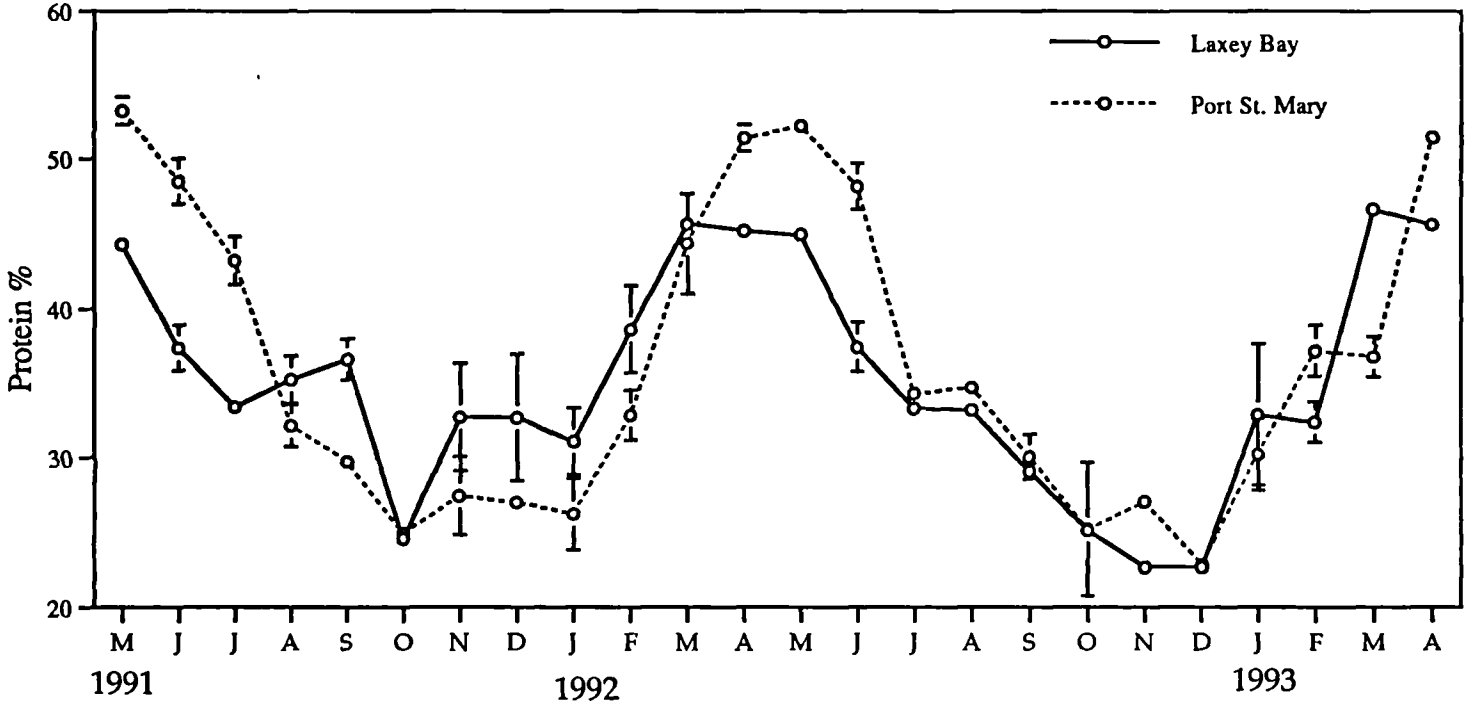


Fig. 3.20a. Seasonal variation in the percentage composition of protein in the digestive gland of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

populations. There was little difference in phase of the seasonal cycles for the two populations but the percentage protein rose to a significantly higher level ($p < 0.05$) in animals from the Port St. Mary ground, compared with Laxey Bay animals, in the period May - June 1991 and April - June 1992.

The absolute protein content of the average digestive gland increased during the spring and summer and reached a maximum in August and September for the two populations in both 1991 and 1992 (Fig.3.20b). The weight decreased during the winter and reached its lowest level in January and February for both populations. The content of protein rose to a much higher level in animals from the Port St. Mary ground in 1991, compared with Laxey Bay animals, and remained at a higher level until August 1992, after which the protein contents of samples from the two grounds were very similar.

b. Lipid

The percentage composition and the absolute content of lipid in the digestive gland varied in a similar manner to the variation of dry weight of the digestive gland during the two year period and showed a very clear seasonal cycle. The percentage of lipid (Fig. 3.21a) rose to high levels in October -December and was lowest during March - May. The level of lipid fluctuated 4% - 33% and 5% - 34% for the animals from Laxey Bay and the Port St. Mary ground respectively. During the first sampling year (May 1991 - May 1992) the lipid levels were significantly higher ($p < 0.05$) in the Laxey Bay population, compared with the Port St. Mary population, during the period June - September and again in December but thereafter the cycles were very similar in phase and amplitude on the two grounds.

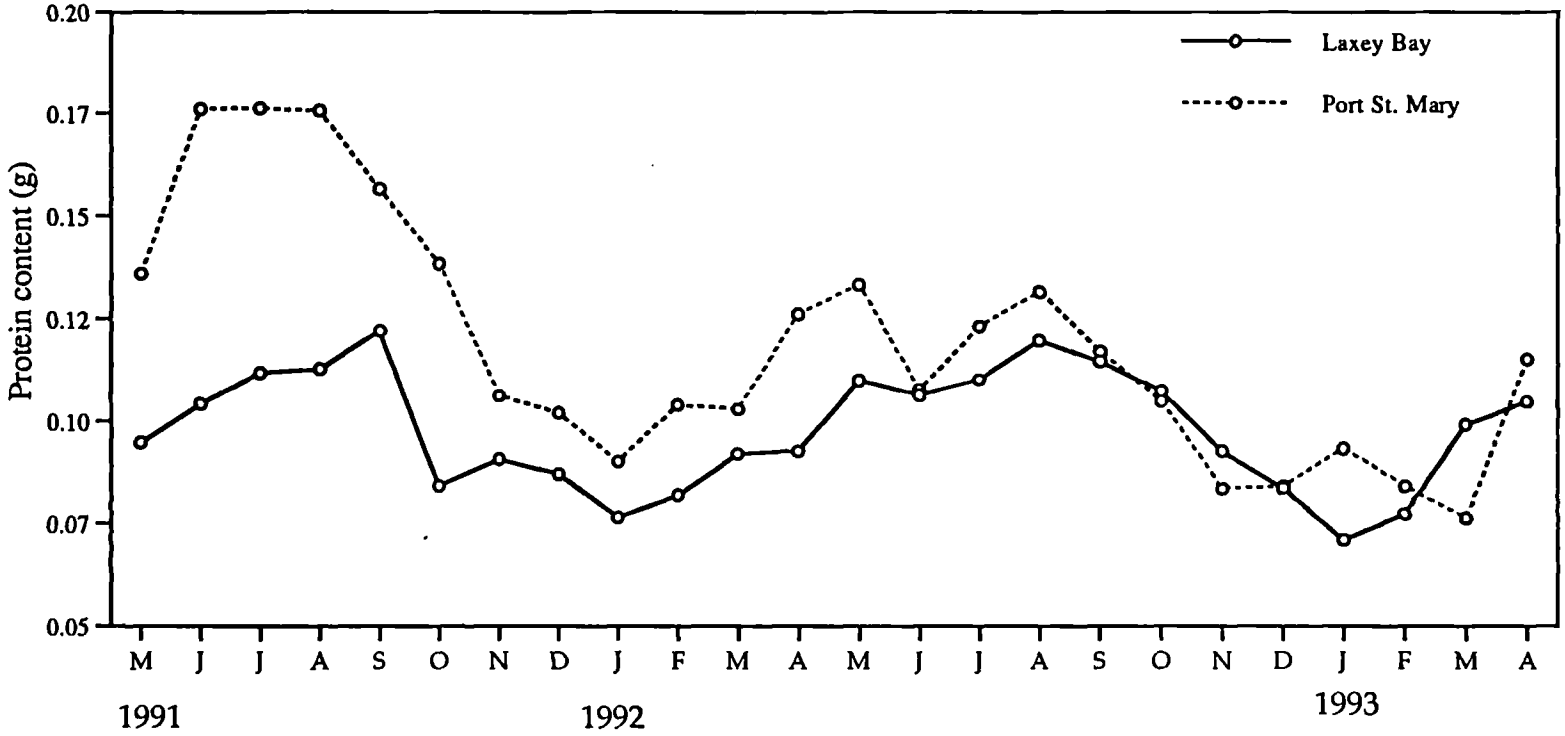


Fig .3.20b. Seasonal variation in the protein content in the digestive gland of *Aequipecten opercularis* (65 - 70 mm shell lenght) from Laxey Bay and Port St. Mary (n = 10 - 15).

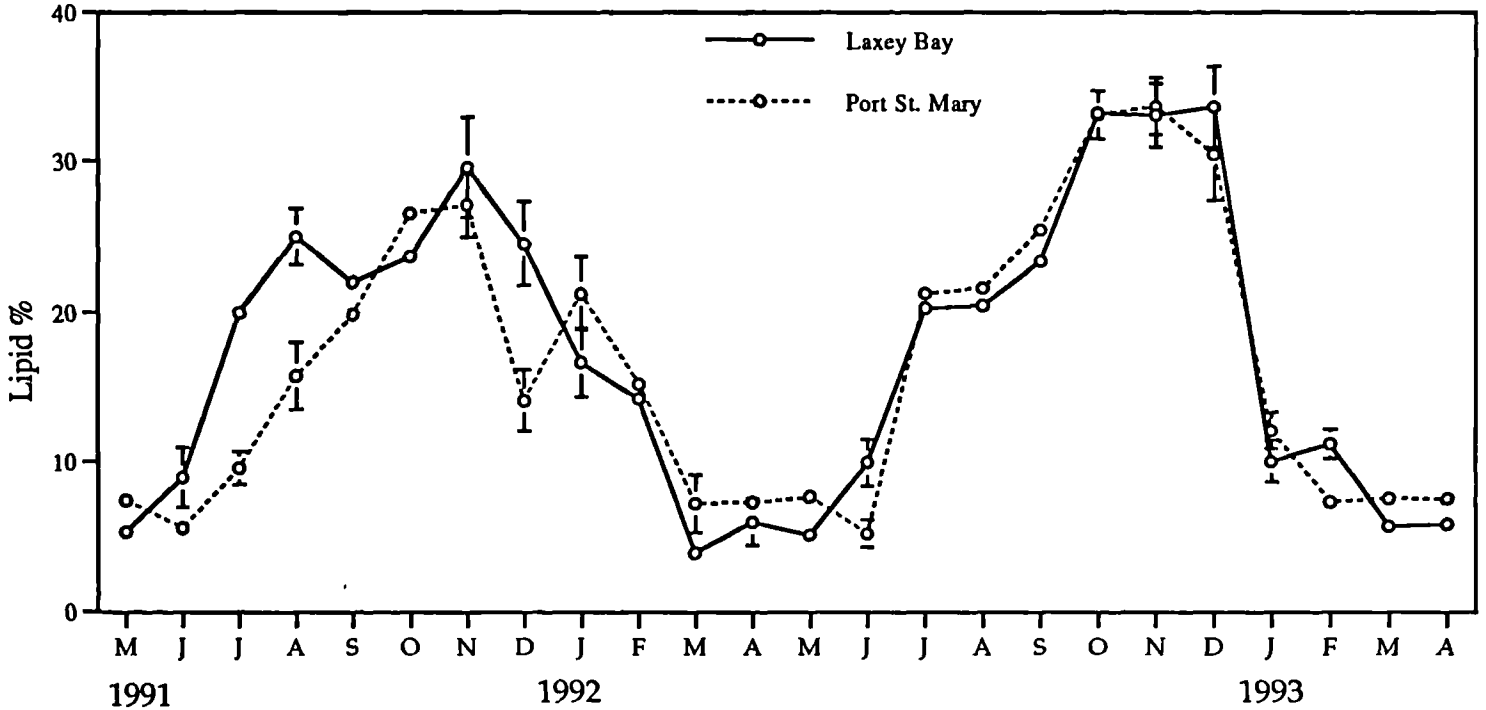


Fig. 3.21a. Seasonal variation in the percentage composition of lipid in the digestive gland of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

The lipid content varied from 0.008g - 0.142g and 0.016g - 0.138g for the *A. opercularis* from Laxey Bay and Port St. Mary respectively, but rose to a higher level for animals from the Port St. Mary ground during the first year sampling period (Fig. 3.21b).

c. Glycogen

The percentage composition and the absolute content of glycogen in the digestive gland were low and variable over the two year period for both populations and showed no clear seasonal variation (Fig. 3.22a, b). The level of glycogen for *A. opercularis* from Laxey Bay varied from 2% - 8% and for the Port St. Mary ground from 3% - 10% (Fig. 3.22a). The absolute content of glycogen followed a similar very variable pattern to the percentage composition and the weight ranged from 0.016g - 0.025g and 0.010g - 0.034g for the animals from Laxey Bay and Port St. Mary respectively (Fig. 3.22b). The highest glycogen contents were noted in June 1991 and October 1992 for the samples from the Port St. Mary ground, but otherwise the only noteworthy feature was the low glycogen contents recorded for samples from both grounds in December 1992.

d. Ash

The ash weight of the digestive gland was not determined separately but only combined with the mantle and gill. The combined ash weight of these 'other tissues,' expressed as percentage composition and absolute content, was relatively high throughout the period of the study, compared with the other body components (Fig.3.23). The monthly values were rather variable between individuals, with relatively high 95% confidence limits, but a seasonal trend of increasing ash content in the summer and decreasing in

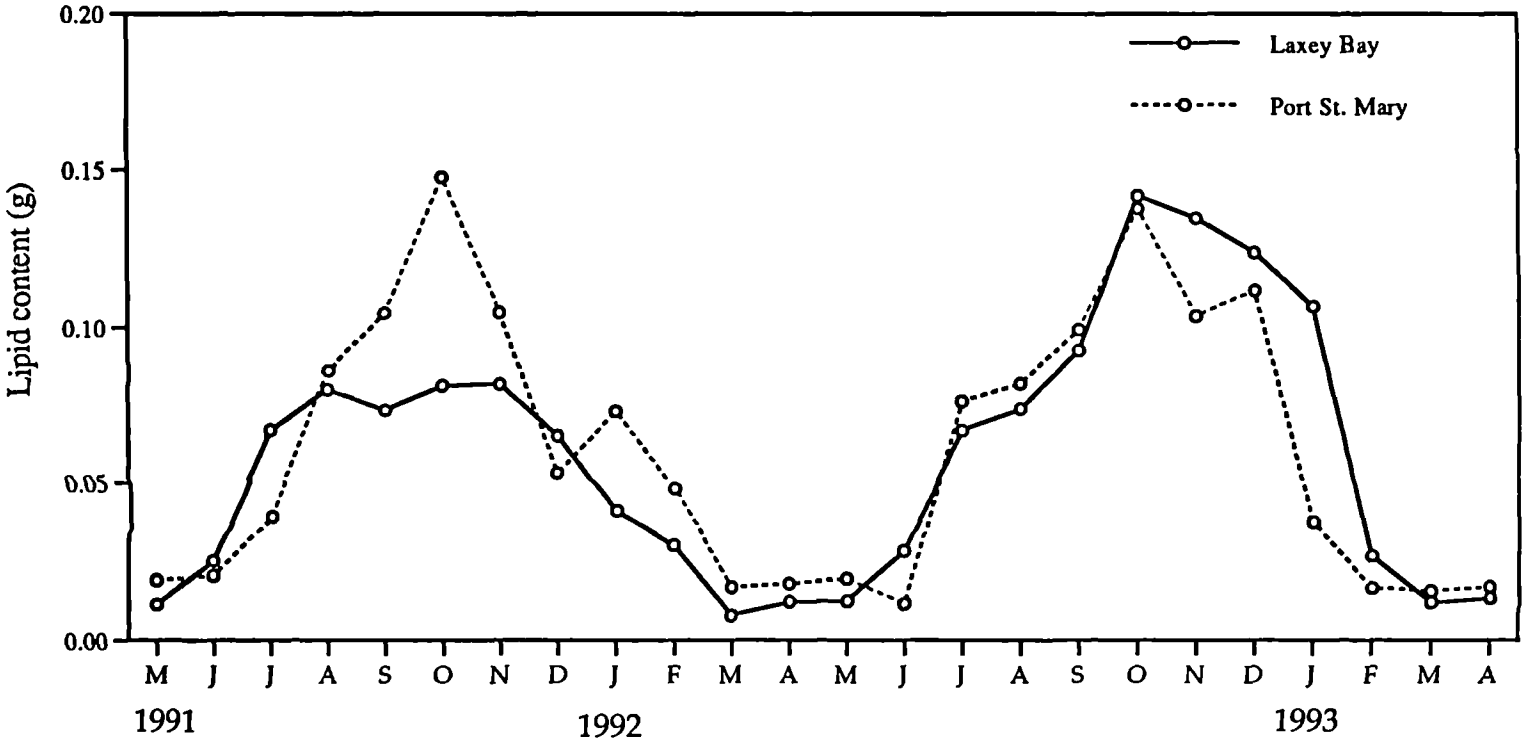


Fig. 3.21b. Seasonal variation in the lipid content in the digestive gland of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary (n = 10 - 15).

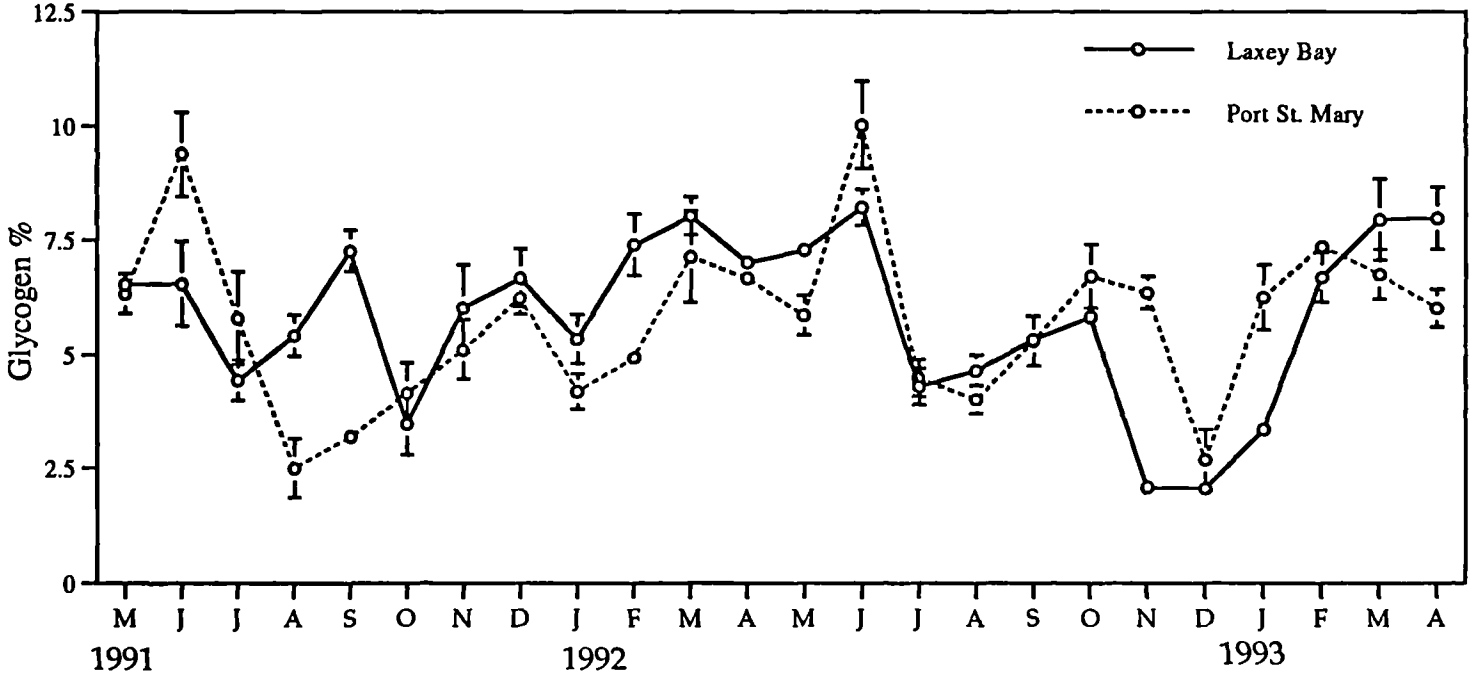


Fig. 3.22a. Seasonal variation in the percentage composition of glycogen in the digestive gland of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 -15).

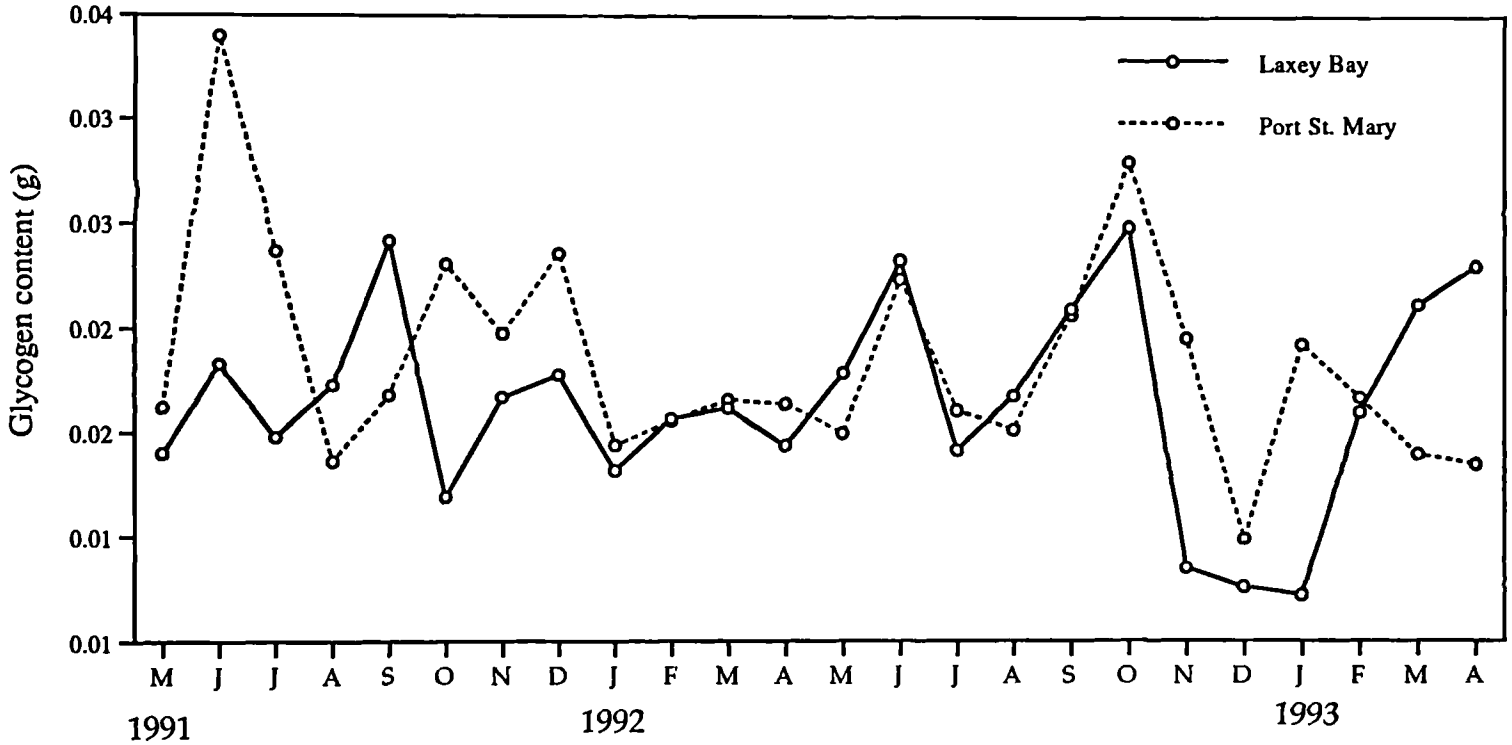


Fig .3.22b. Seasonal variation in the glycogen content of the digestive gland of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary (n = 10 - 15).

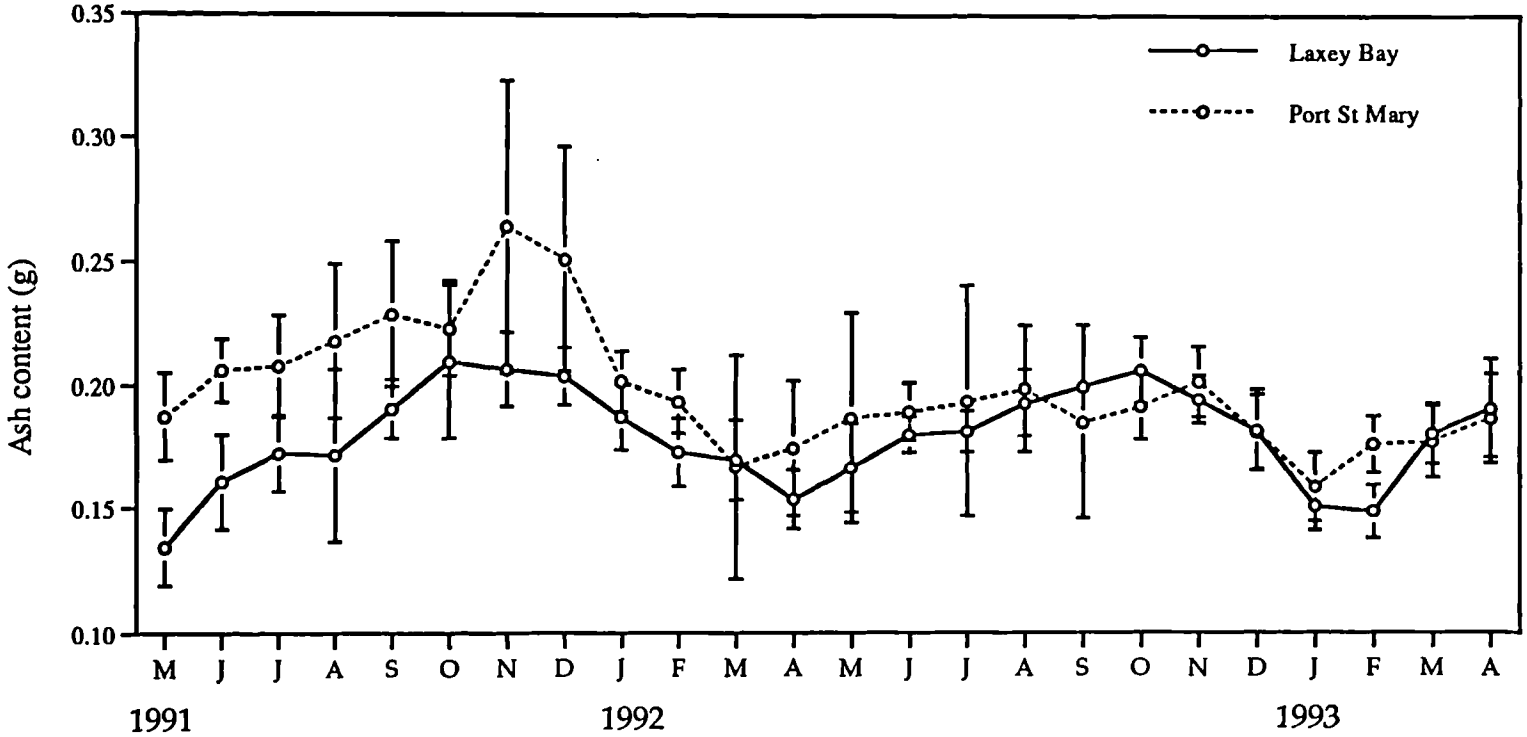


Fig. 3.23. Seasonal variation in the 'other tissue' (mantle tissue, gills, digestive gland) ash weight of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals.

the winter was evident. There was some indication also of a higher ash content in the Port St. Mary population, compared with the Laxey Bay population, throughout 1991 although only the May and June paired values were significantly different ($p < 0.05$).

e. Water

The percentage water content of the digestive gland followed similar seasonal patterns to the water content of the adductor muscle throughout the study (Fig. 3.24). The lowest water content was noted at both sites during the early autumn, while the highest values were in late winter and early spring. The digestive gland showed the lowest level of water compared with other tissue components which varied from 68% to 79% for the two populations.

3.3.1.5 Percentage of total water

The variation in the percentage water of all the tissues of *A. opercularis* combined (Fig.3.25) showed a similar variation to that of the adductor muscle (Fig.3.6), which contributes a major part to the body tissues. The percentage of water was lowest during the summer and early autumn and highest in the winter and early spring for both populations. During the period October 1991 to March 1992, the percentage water contents of the samples from Laxey Bay were significantly ($p < 0.05$) higher than for the samples from the Port St. Mary ground.

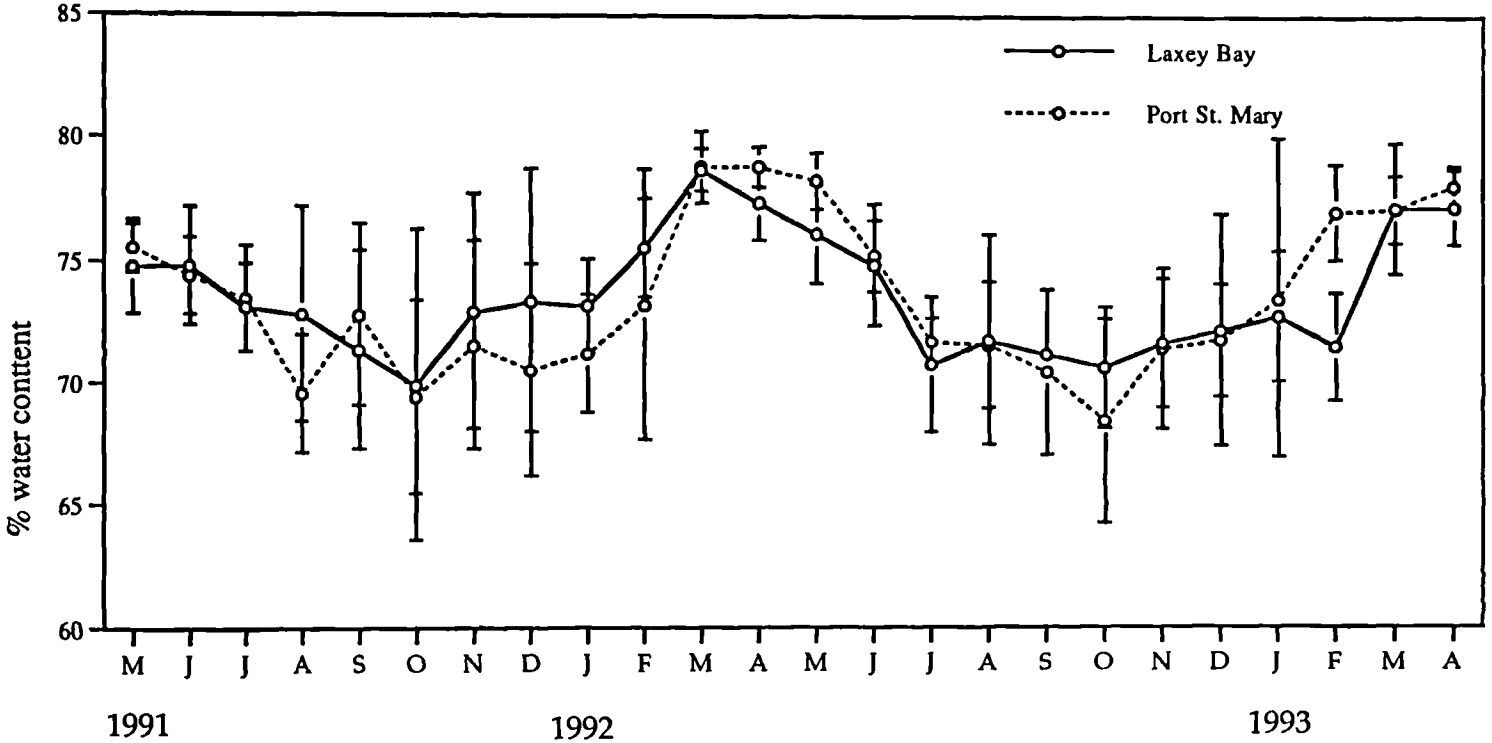


Fig. 3.24. Seasonal variation in the percentage water content of the digestive gland of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary Values represent means and 95% confidence intervals.

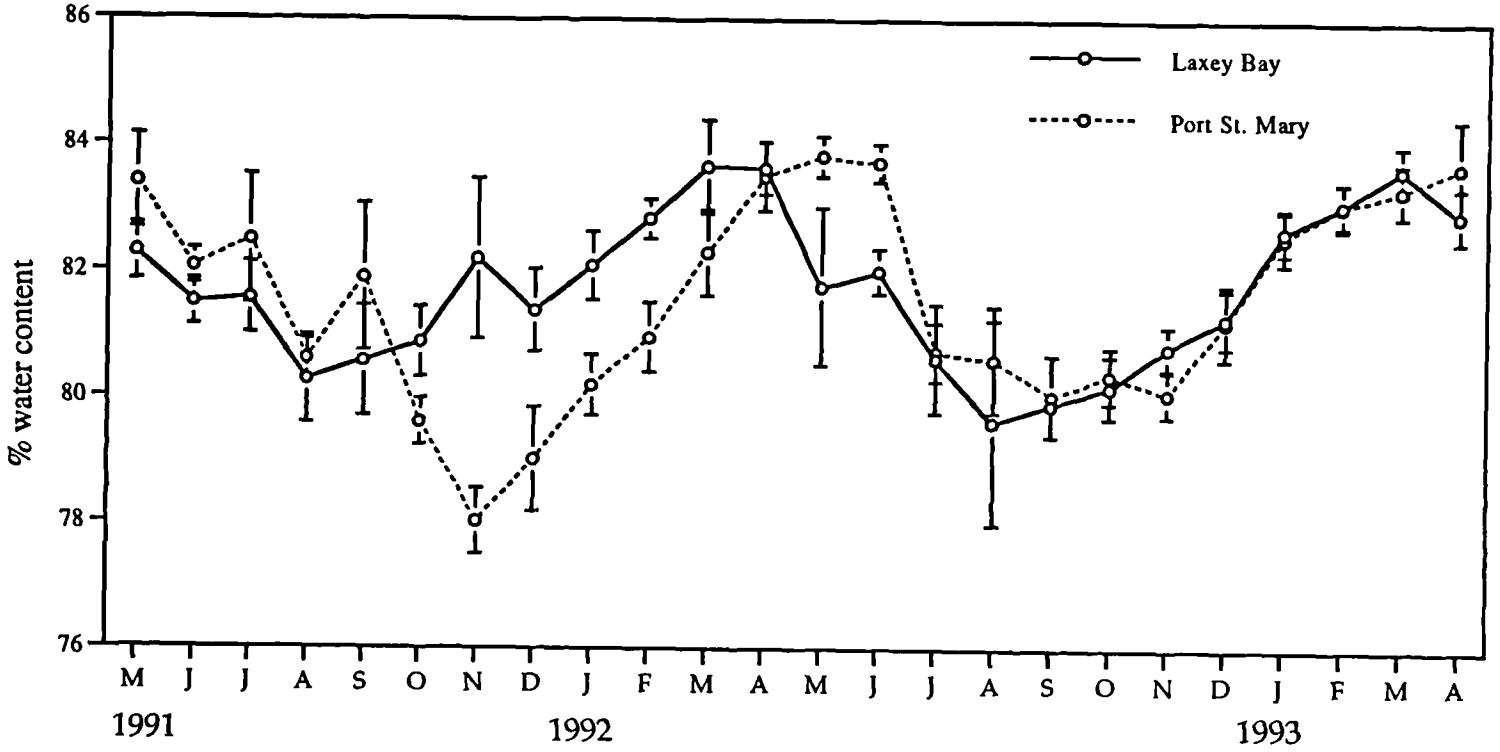


Fig. 3.25. Seasonal variation in the percentage water content of the total tissue of *Aequipecten opercularis* (65 - 70 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals.

3.3.2. Biochemical composition of *Pecten maximus*

3.3.2.1 Adductor muscle

a. Protein

The percentage of protein in the adductor muscle of *Pecten maximus* from the two populations (Fig.3.26a) followed a similar seasonal variation to the adductor muscle of *A. opercularis* over the two year period. There was a decrease in the percentage protein in both populations during the autumn and winter but it then rose rapidly to reach its maximum level in March and April. Scallops from Laxey Bay showed slightly higher protein levels, ranging from 62% - 76%, while the Port St. Mary population ranged from 62% - 74%. The percentage protein was significantly higher in Laxey Bay scallops ($p < 0.05$) in the months of April and December 1991, and January and August 1992, but thereafter the pattern changed and during the period November 1992 to February 1993 the percentage of protein was significantly higher ($p < 0.05$) in the samples from the offshore Port St. Mary ground.

The absolute protein content of the average adductor muscle increased during the summer to reach its maximum weight in September (1991) or November (1992); it then decreased over the winter to the minimum weight in February or March (Fig. 3.26b). The absolute protein content in the adductor muscle of *P. maximus* was high compared to the rest of the tissues and varied from 4.40g - 6.21g and 4.85g - 6.15g for animals from Laxey Bay and Port St. Mary respectively.

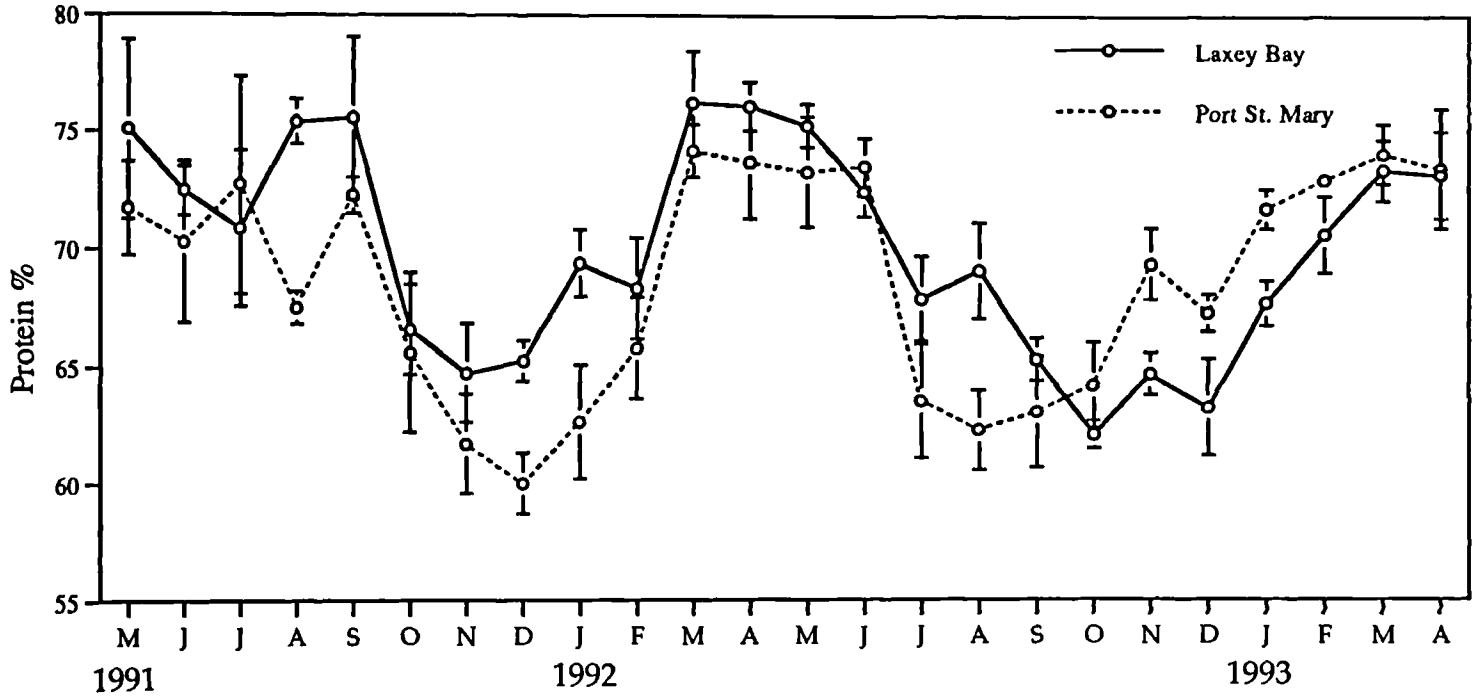


Fig. 3.26a. Seasonal variation in the percentage composition of protein in the adductor muscle of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appeared on the graph (n = 10 - 15).

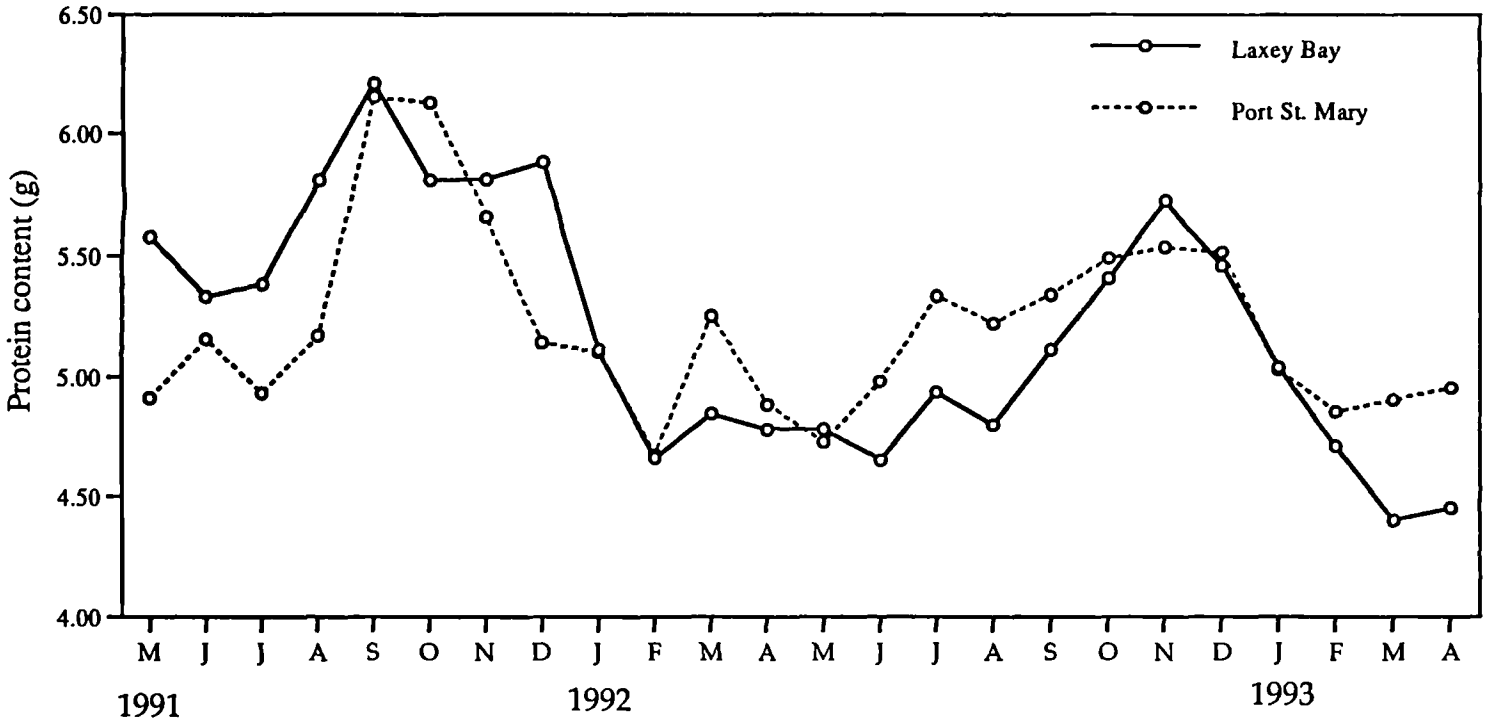


Fig. 3.26b. Seasonal variation in the protein content of the adductor muscle of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary (n = 10 - 15).

b. Lipid

The percentage of lipid in the adductor muscle remained at a low level of 2% - 3.5% for the whole of the study period for both populations and did not indicate clear seasonal variations (Fig. 3.27a). The absolute content of lipid in the adductor muscle was low, ranging from 0.16g - 0.32g throughout the period for the both populations (Fig. 3.27b), but there was a clear seasonal cycle, rising to a maximum in October, November or December and falling to a minimum in April or May. The cycles were of similar amplitude on the two grounds but there was some indication that the build- up and subsequent decline of lipid occurred 1-2 months earlier in the Port St. Mary population in 1992, compared with the Laxey Bay population.

c. Glycogen

Adductor muscle glycogen in *P. maximus* showed large seasonal variations similar to the variation of *A. opercularis*.

The percentage of glycogen ranged from 6.1% - 16.18% and 6.64% - 15.5% for the animals from Laxey Bay and Port St. Mary respectively (Fig.3.28a). The percentage levels were lowest in late winter and early spring (February and March) and highest in late summer and early autumn. In the first year of sampling, the percentage of glycogen was significantly higher ($p < 0.05$) in August 1991 and January - February 1992 in the scallops from the Port St. Mary ground. However, this position changed in the second year and from October 1992 onwards, glycogen levels were higher in animals from Laxey Bay.

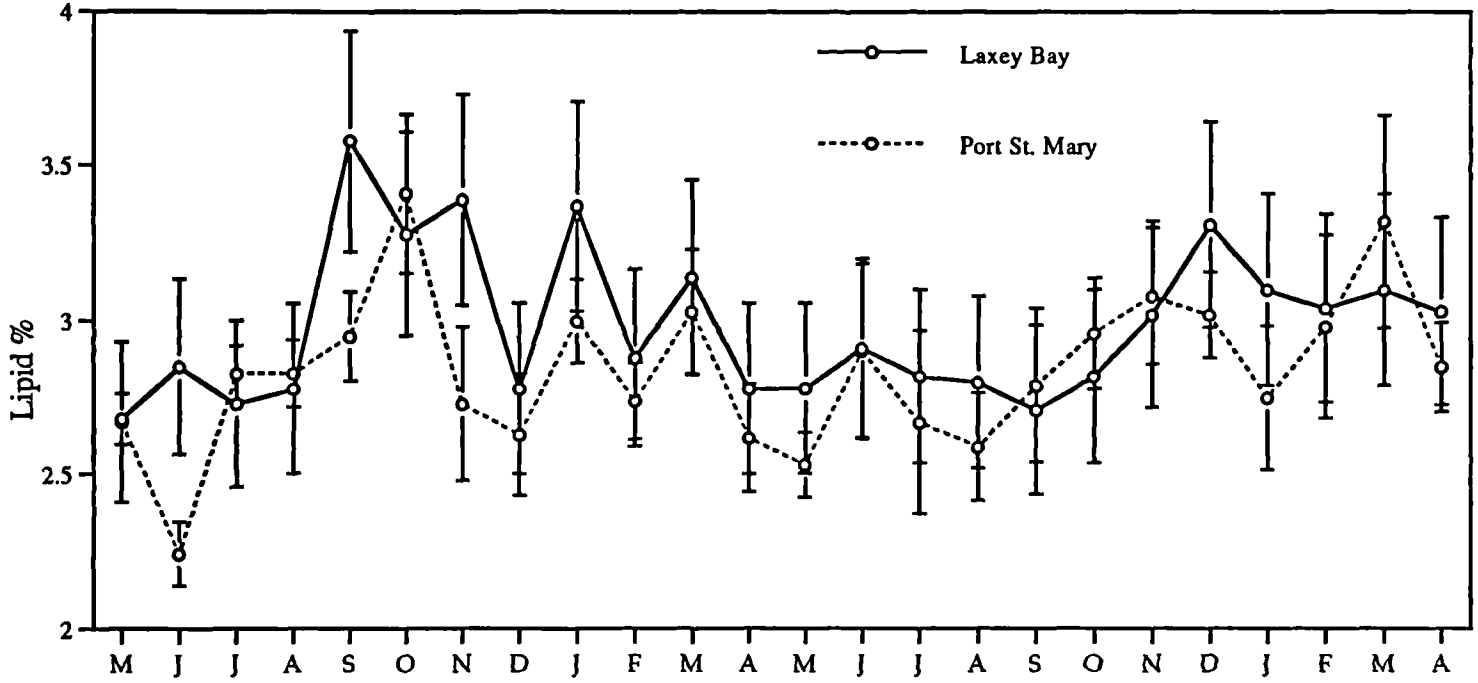


Fig. 3.27a. Seasonal variation in the percentage composition of lipid in the adductor muscle of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals (n = 10 - 15).

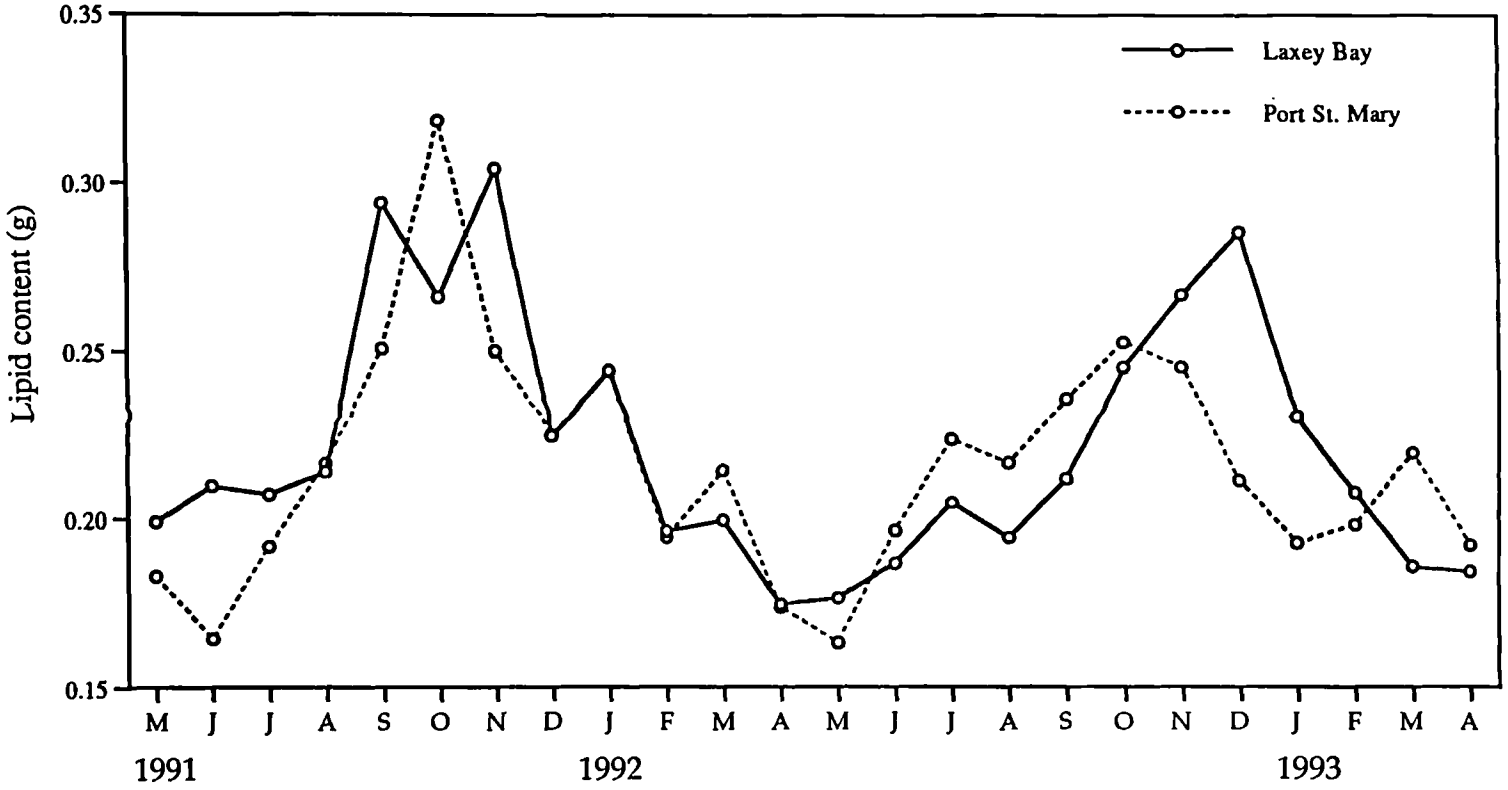


Fig. 3.27b. Seasonal variation in the lipid content of the adductor muscle of *Pecten maximus* (120 -130 mm shell length) from Laxey Bay and Port St. Mary (n = 10 - 15).

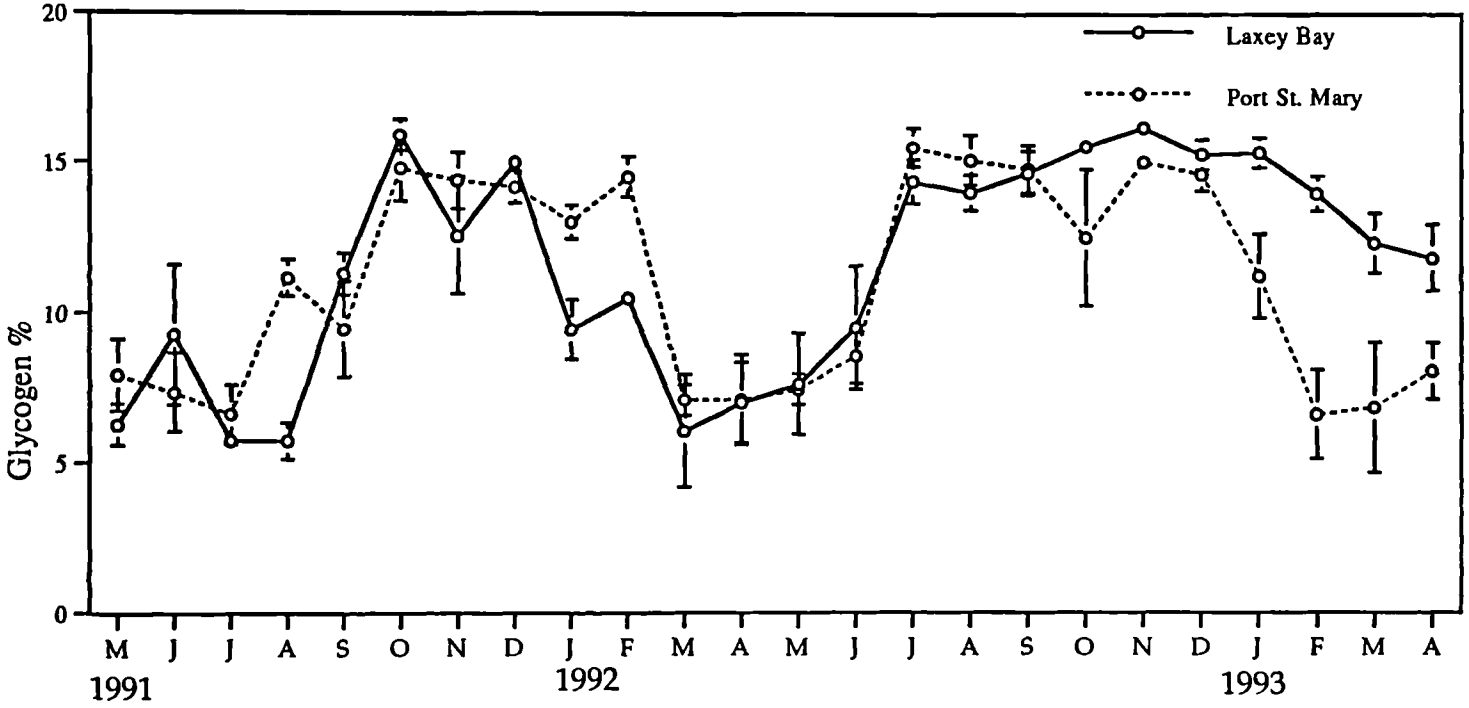


Fig. 3.28a. Seasonal variation in the percentage composition of glycogen in the adductor muscle of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graphs (n = 10 - 15).

The absolute content of glycogen also showed a very clear seasonal cycle and followed a similar pattern to the variation for the percentage glycogen (Fig. 3.28b) with the highest levels in autumn and lowest in early spring.

d. Ash

Fig. 3.29 shows seasonal variation in the ash weight of the adductor muscle of *P. maximus* from the Laxey Bay and Port St. Mary grounds. Some seasonal fluctuation was apparent, with ash weight highest in September-November and lowest in March - May. Ash weight was generally higher for the Laxey Bay population but individual variation was high and only the paired values for October 1991 were significantly different ($p < 0.05$). The percentage level of ash followed a similar pattern to the content of ash for both populations and ranged from 6% - 13% throughout the two year period.

e. Water

The percentage water content in the adductor muscle of *Pecten maximus* (Fig. 3.30) varied in a similar manner to the changes in water content of *Aequipecten opercularis*. The animals from Laxey Bay showed the lowest percentage water in November 1991 (74.77%) and October 1992 (74.13%); the highest water content was in March 1992 (78.82%) and April 1993 (77.55%). Similarly, scallops from the Port St. Mary ground had their minimum water content in October 1991 and 1992, and the maximum water content was reached in April 1992 and February 1993. The seasonal fluctuation in water content was therefore about 4% - 5% in the adductor muscle at both sites. The percentage water levels were significantly higher

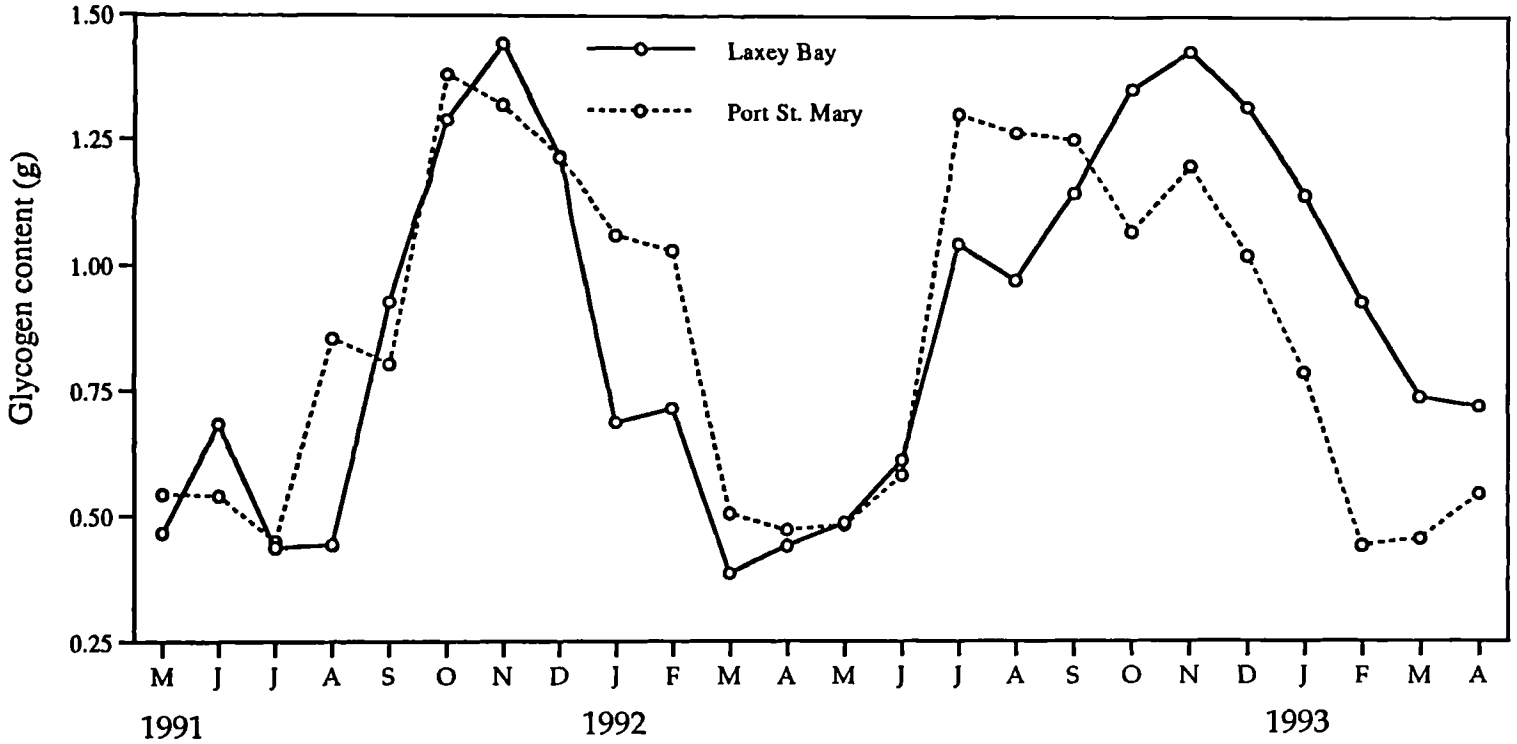


Fig. 3.28b. Seasonal variation in the glycogen content of the adductor muscle of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary (n = 10 - 15).

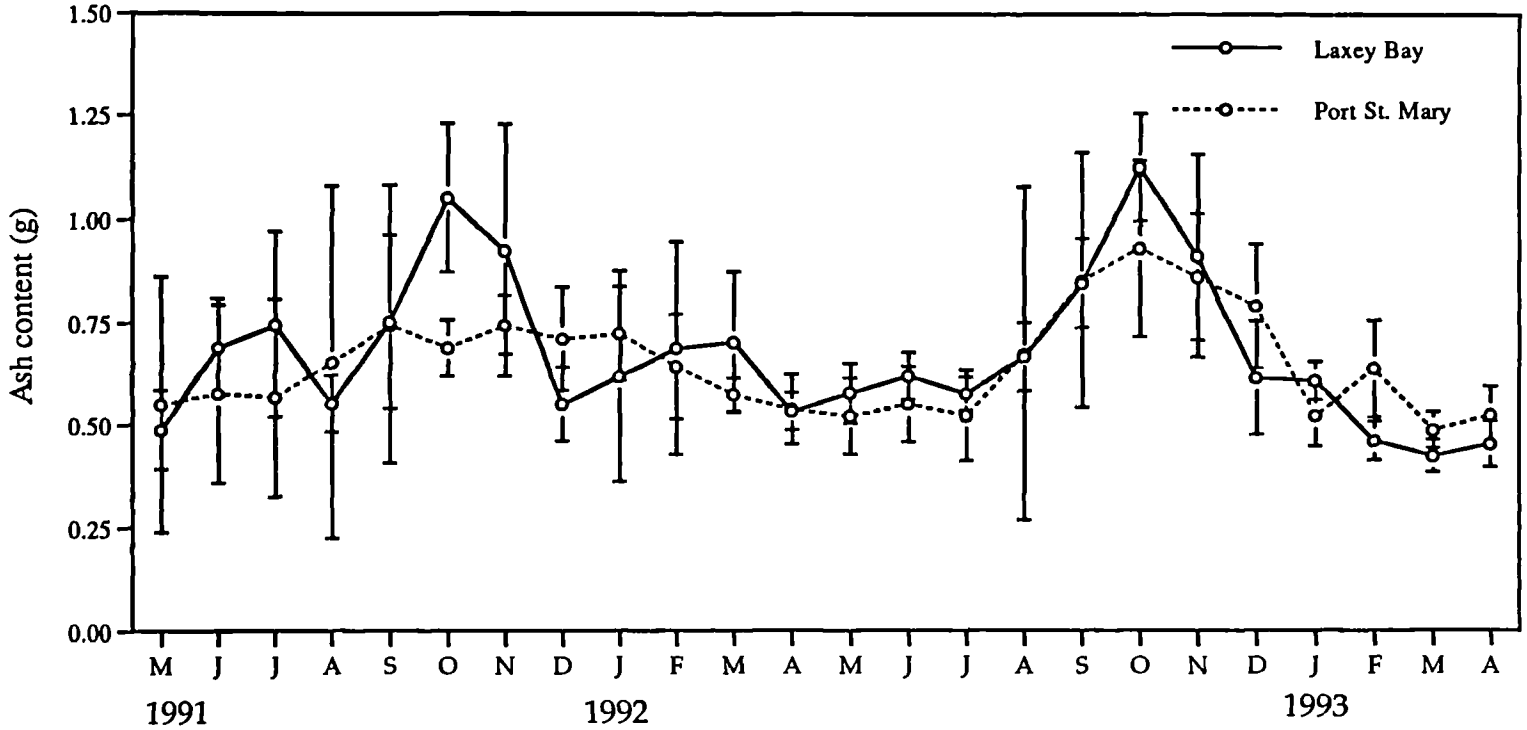


Fig. 3.29. Seasonal variation in the adductor muscle ash content of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals.

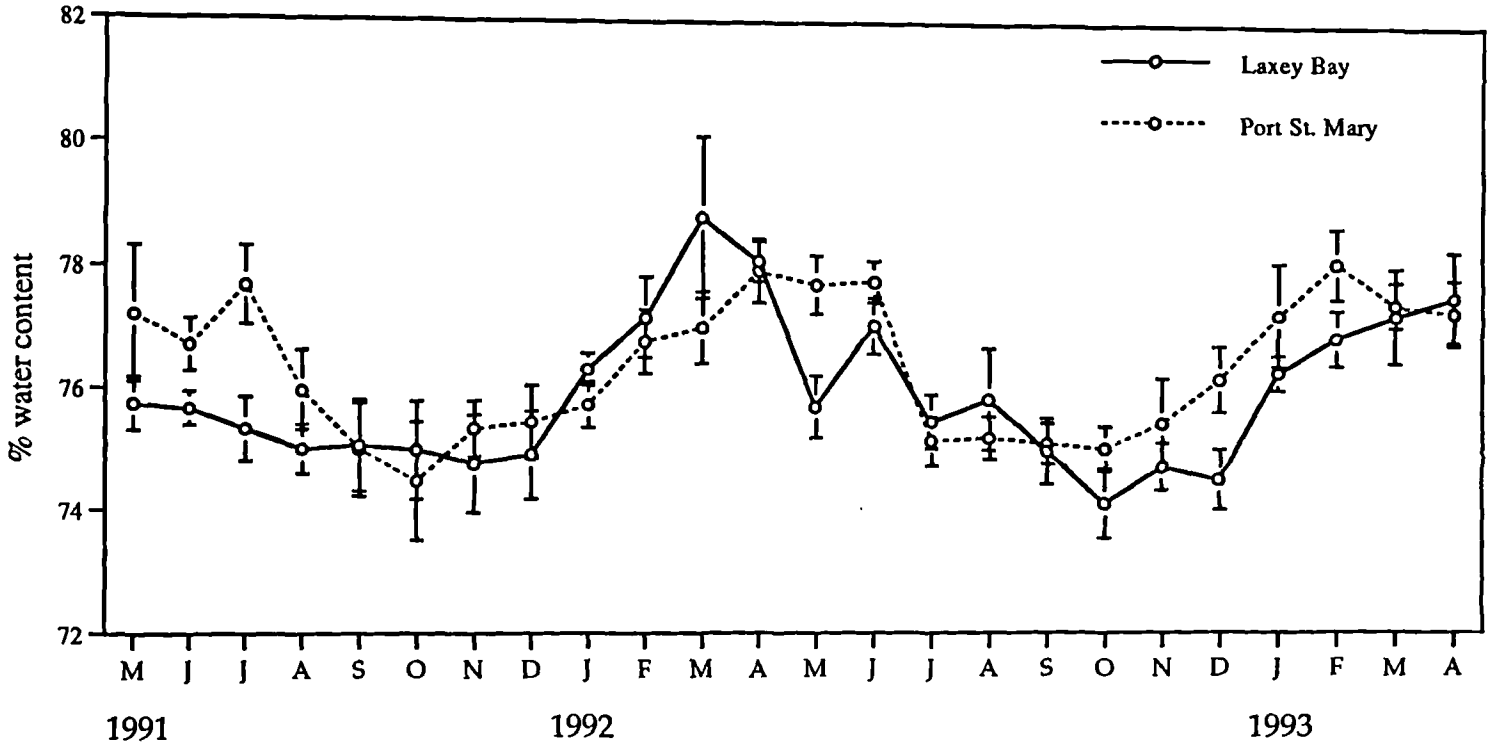


Fig. 3.30. Seasonal variation in the percentage water content of the adductor muscle of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals.

($p < 0.05$) for scallops from the Port St. Mary ground, compared with Laxey Bay, in the periods May - July 1992, May 1992 and December 1992 - February 1993 and there was an indication that the seasonal increase in water content occurred rather earlier in the Port St. Mary population in autumn 1992.

3.3.2.2 Gonad (testis and ovary)

Protein, lipid and glycogen were analysed separately in the testis and ovary portions of the gonad of *P. maximus*, as was done with *A. opercularis*. Percentage values for the separate portions and the combined biochemical contents (testis and ovary together) are illustrated in the figures.

a. Protein

The percentage of protein in the testis increased steadily during gametogenesis in late autumn and winter to a high level in spring in both populations (Fig. 3.31). The seasonal fluctuations were similar on the two grounds and although many of the paired monthly values were significantly different, there were no consistant differences in pattern between the two populations.

The percentage of protein in the ovary was relatively low compared with the testis ranging from 50.24% - 56.33% for animals from Laxey Bay, while for the Port St. Mary ground it varied from 49.56% - 56.67% (Fig. 3.32). The ovary showed a decrease in the percentage of protein with increase in gonad size. This was due to reciprocal increases in the percentage of other biochemical components, especially lipid which was higher in the gonad.

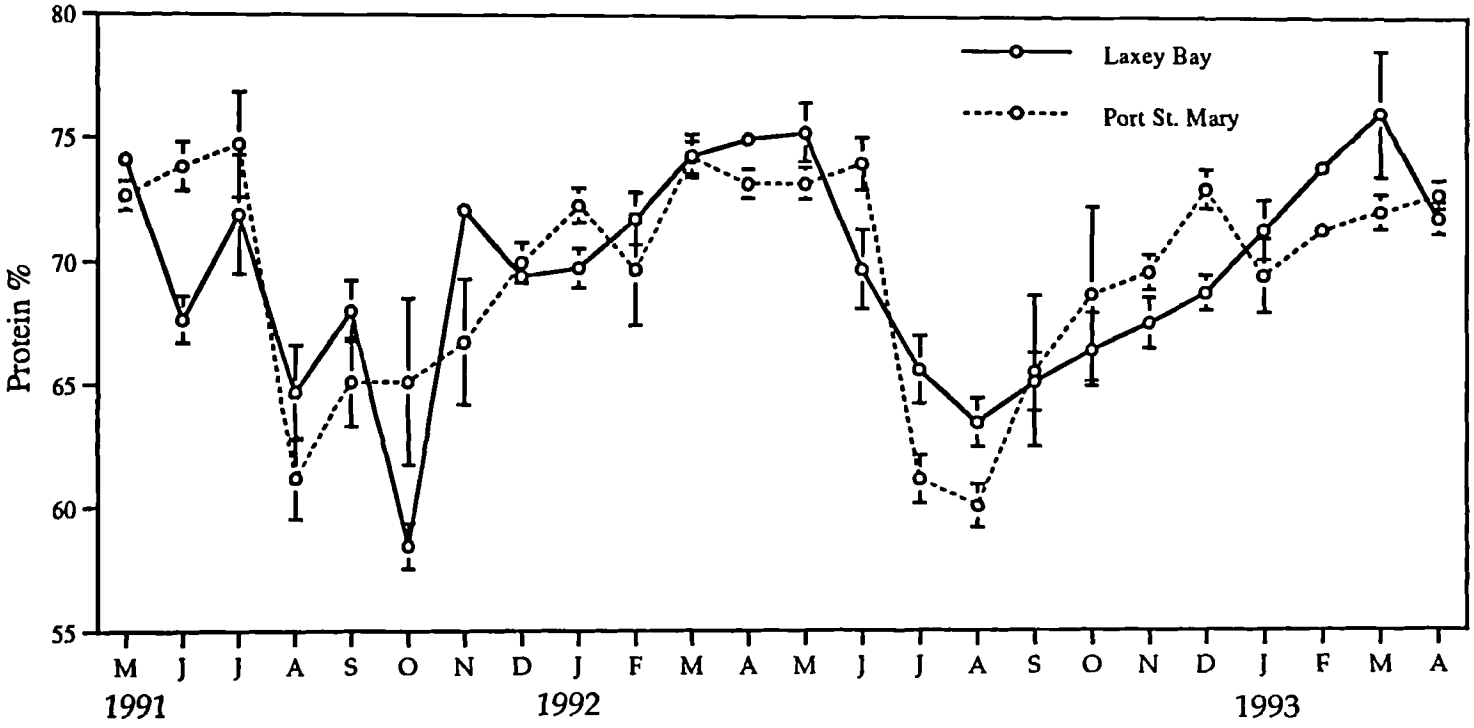


Fig. 3.31. Seasonal variation in the percentage composition of protein in the testis of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and the Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

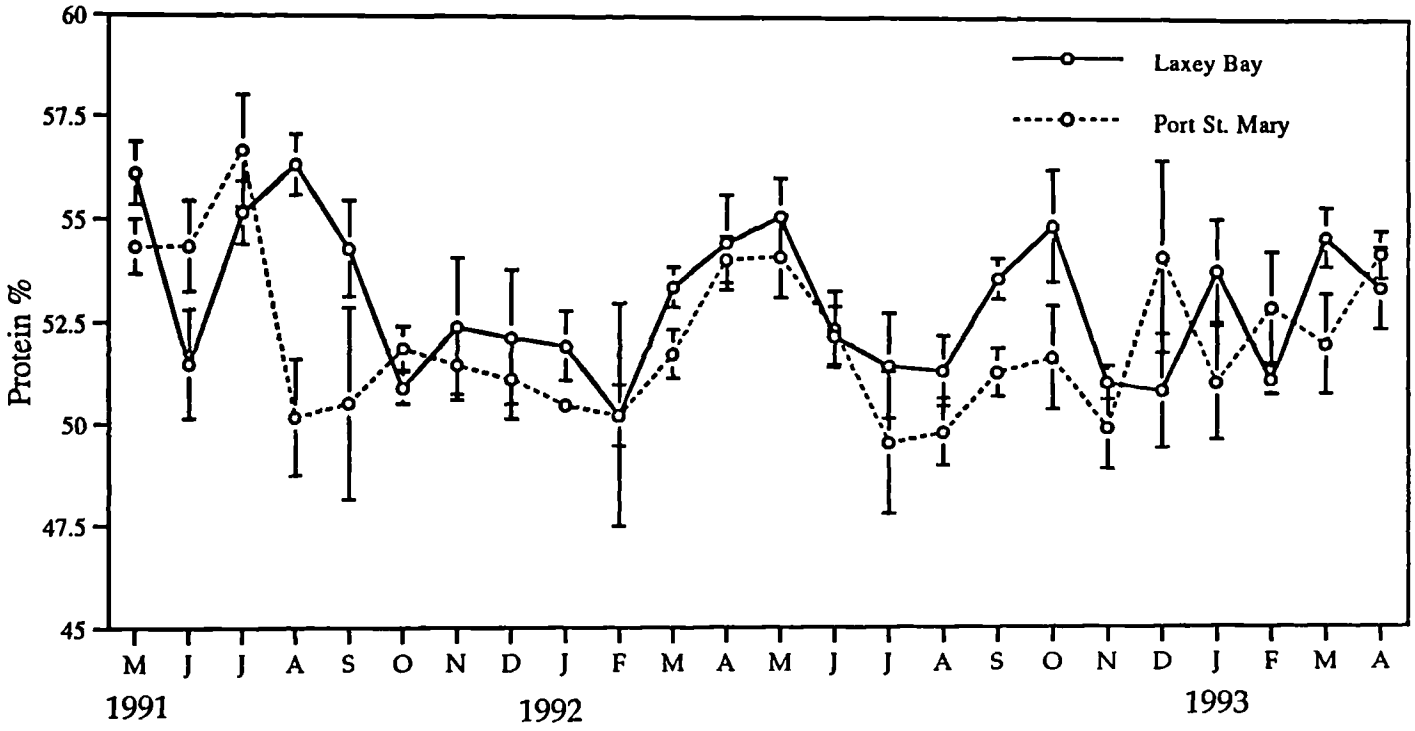


Fig. 3.32. Seasonal variation in the percentage composition of protein in the ovary of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

b. Lipid

The lipid level in the testis remained low, ranging from 4.8% - 8.2% and 3.8% - 8.7% respectively for Laxey Bay and Port St. Mary. It also showed no clear pattern of seasonal variation throughout the period of study (Fig. 3.33), though there appeared to be two or three rapid decreases at both grounds each year.

The percentage lipid in the ovary showed a more clear pattern with two cycles of increasing and decreasing lipid each year on both grounds (Fig. 3.34). These cycles varied somewhat in both amplitude and timing so that the paired values for the two grounds were significantly different ($p < 0.05$) for many months of the year. The lipid levels of the ovaries from the offshore Port St. Mary ground varied over a greater range (5.66% - 18.02%) than the Laxey Bay population (8.21% - 15.35%). Rapid decreases of lipid were observed to correspond with spawning.

c. Glycogen

The glycogen level of both the testis and ovary of *P. maximus* remained at a low level (Fig.3.35 and Fig.3.36) similar to *A. opercularis* (Figs.3.11, 3.12). The lowest levels of glycogen were found in the spent testis and ovary, while the full ovary and testis had the highest levels. The glycogen levels in the testis (Fig. 3.35) were particularly low in August and September 1991 but thereafter increased steadily, particularly on the offshore Port St. Mary ground. As a result, the monthly values recorded for the Port St. Mary samples in the period August - November 1991 were significantly lower (p

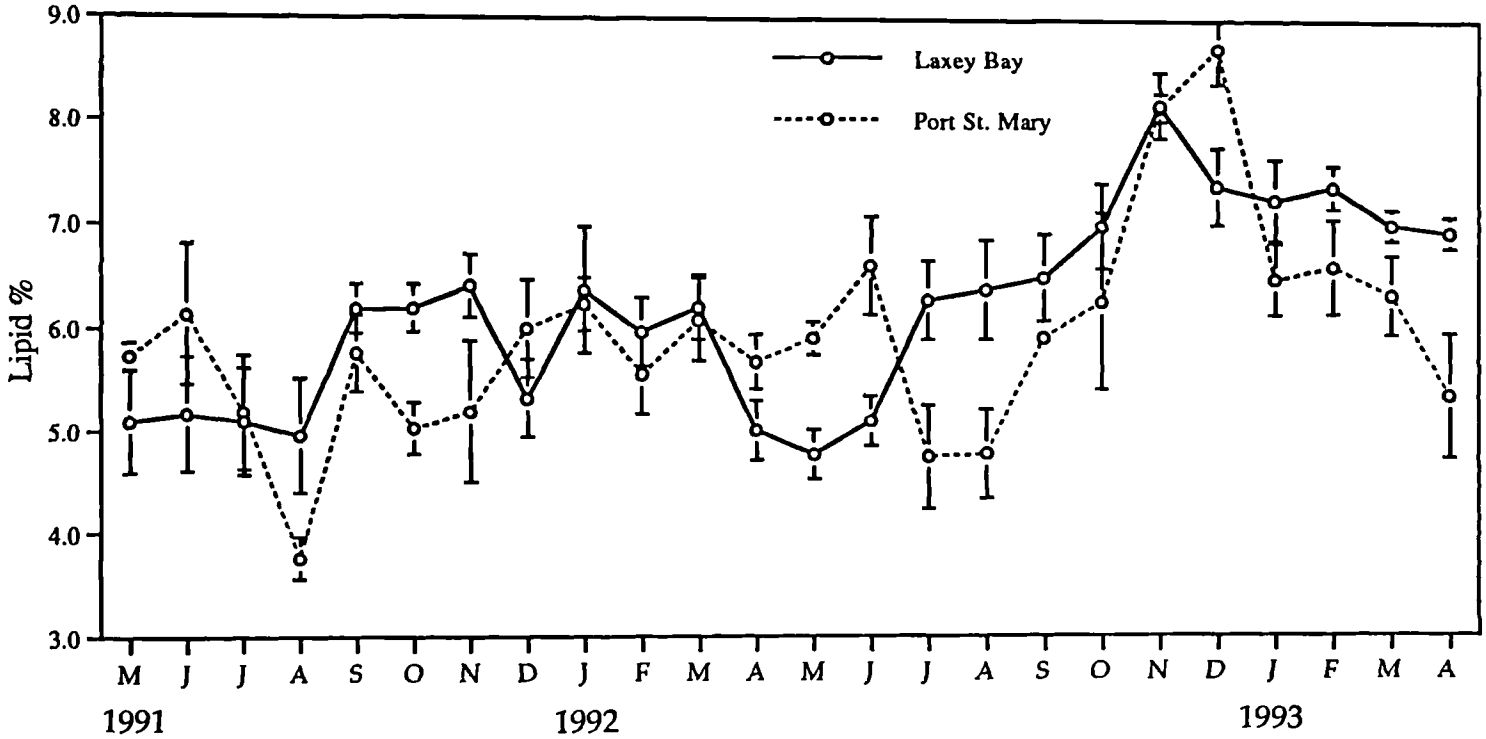


Fig. 3.33. Seasonal variation in the percentage composition of lipid in the testis of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

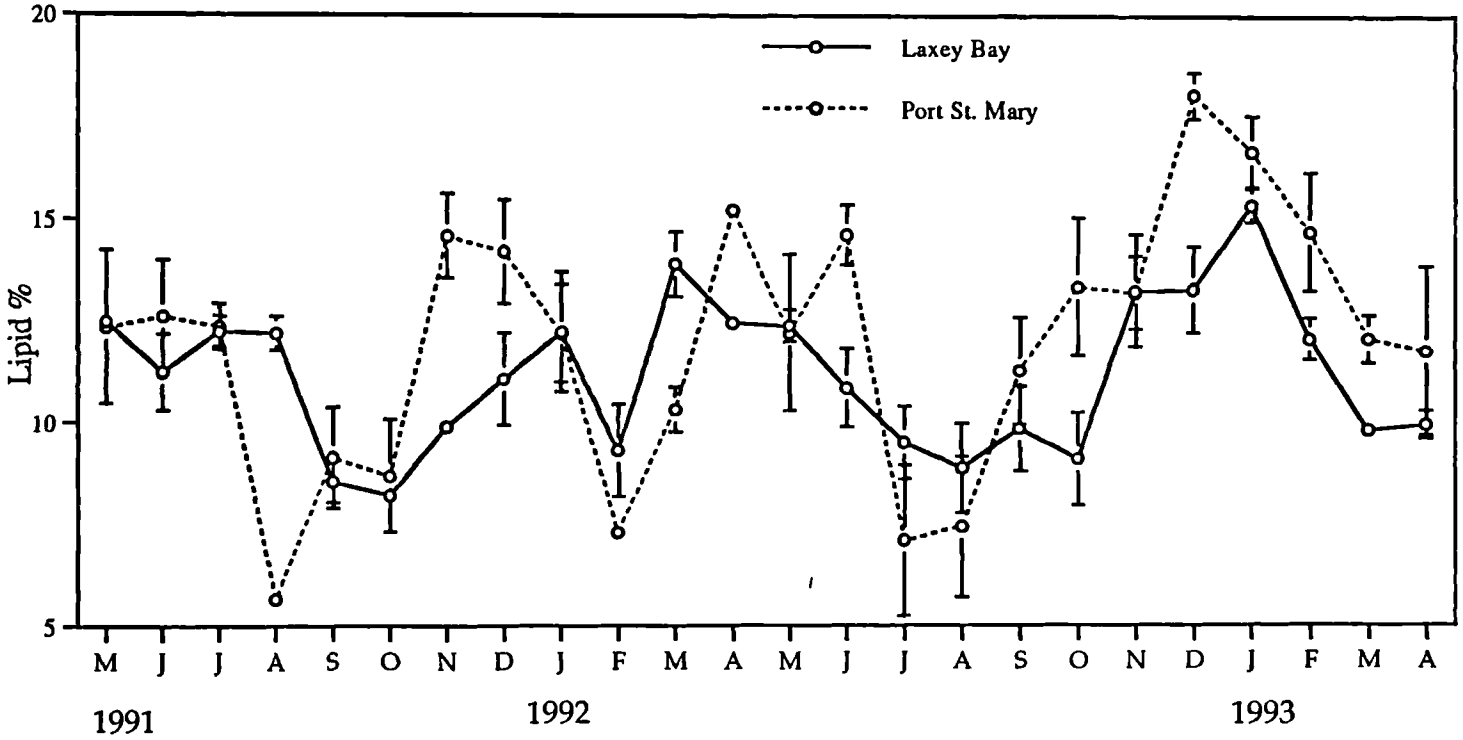


Fig. 3.34. Seasonal variation in the percentage composition of lipid in the ovary of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% c0nfidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

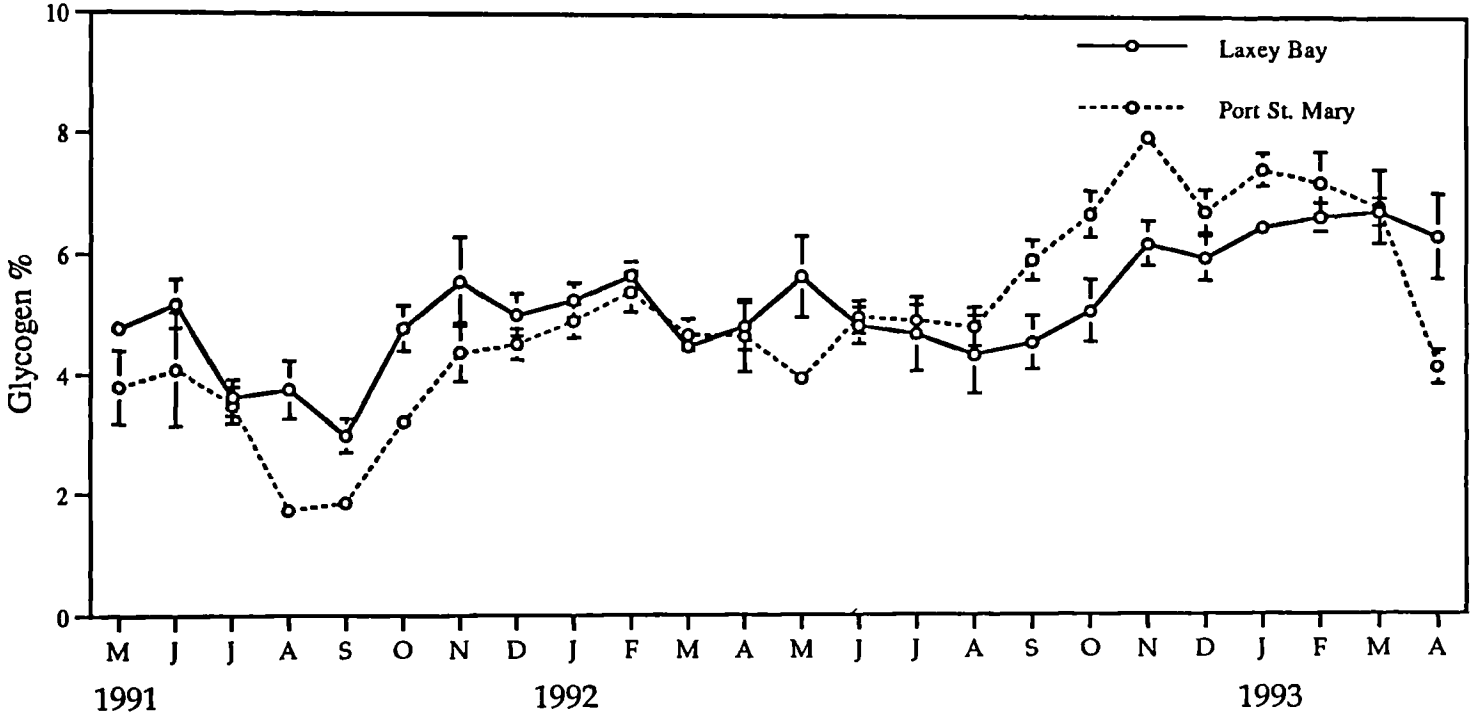


Fig. 3.35. Seasonal variation in the percentage compositon of glycogen in the testis of ***Pecten maximus*** (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

<0.05) than the Laxey Bay samples but the position then reversed and from September 1992 until January 1993 they were significantly higher ($p < 0.05$).

The percentage of glycogen in the ovary followed the same pattern, falling in spring and summer and rising in autumn and winter and with the 1992 - 93 values significantly higher for the offshore Port St. Mary ground (Fig.3. 36). The glycogen levels recorded in the ovary were generally slightly higher than in the testis throughout the study.

d. Absolute biochemical composition

Fig. 3.37 shows the seasonal variation in the contents of protein, lipid and glycogen in the gonad (testis and ovary combined) of the populations from the two grounds. As in *Aequipecten opercularis*, the pattern of seasonal changes followed that of the gonad dry weight (Fig. 1.13) throughout the period. During the winter, due to gametogenesis, the biochemical contents increased gradually and reached its maximum prior to spawning for both populations and after spawning the contents decreased immediately to the minimum level. This is very clearly illustrated by the changes of protein contents in the gonadal tissues. The build-up of biochemical contents showed time differences which indicate that there were some differences in gametogenesis and spawning between *P. maximus* populations from the two grounds during the study period.

e. Ash

The ash weight of gonad (testis and ovary combined) (Fig.3.38) showed a similar seasonal variation to the dry weight of gonad (Fig.1.15). The lowest ash weight was observed in the spent gonad and the highest values were

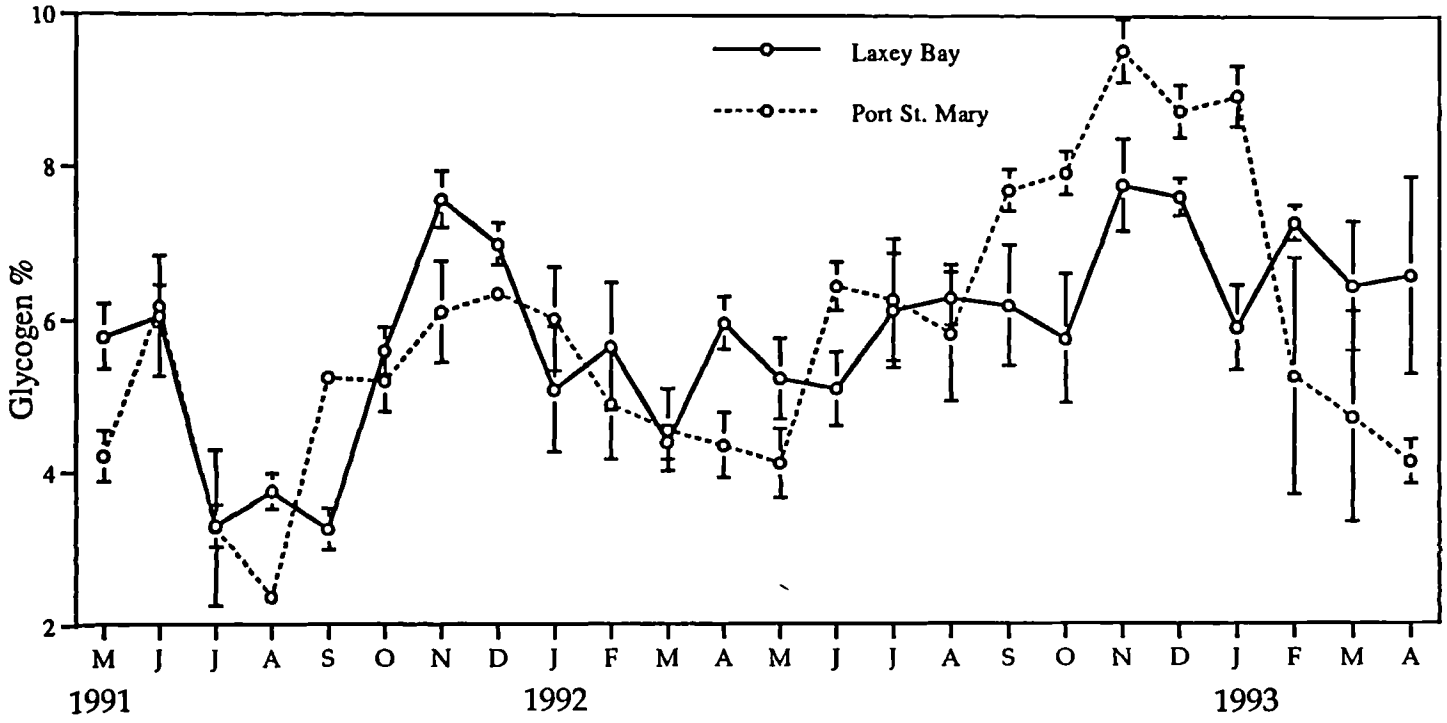


Fig. 3.36. Seasonal variation in the percentage composition of glycogen in the ovary of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

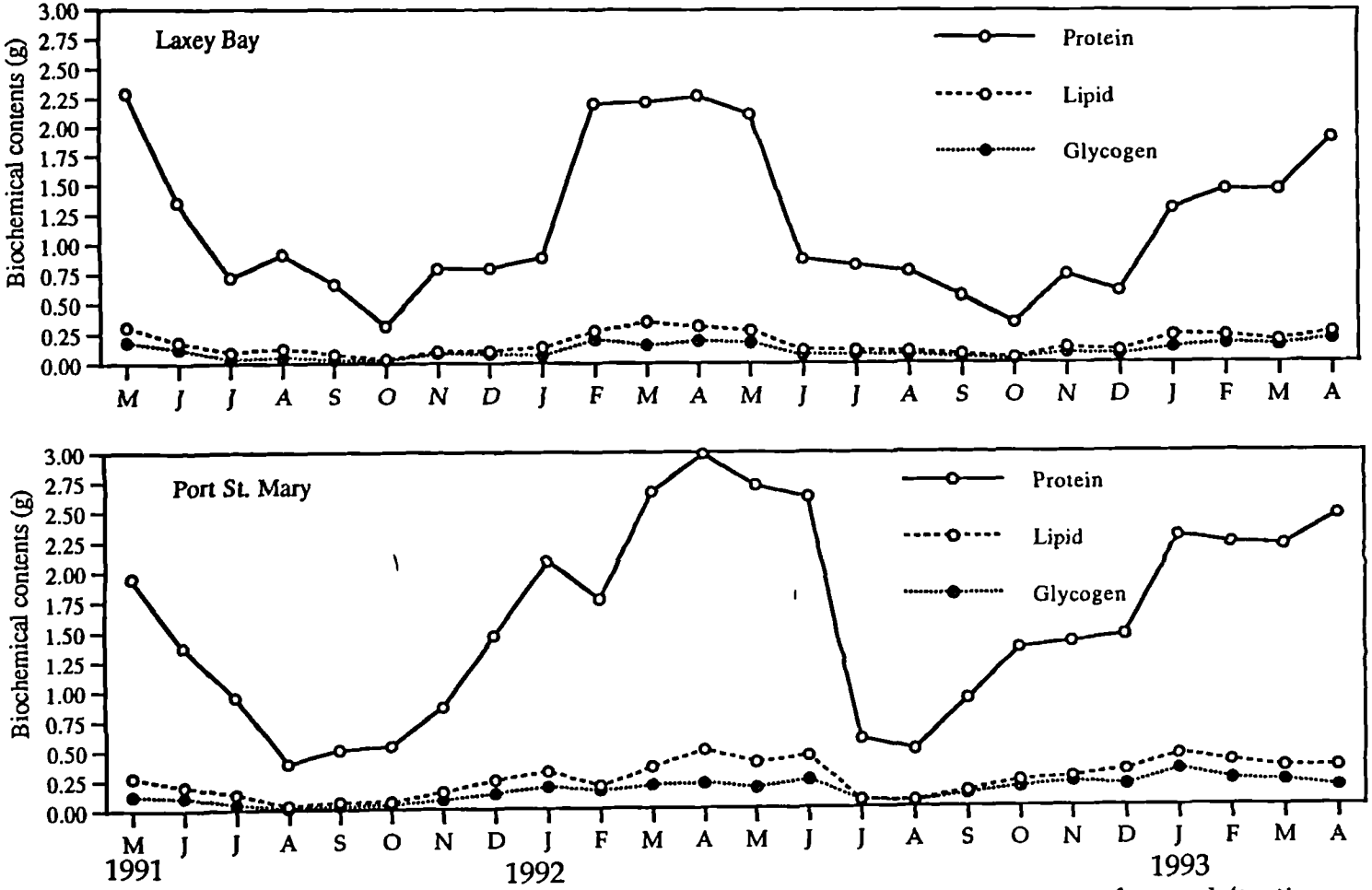


Fig.3.37. Seasonal variation in the protein, lipid and glycogen contents of gonad (testis and ovary combined) of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary (n = 10 - 15).

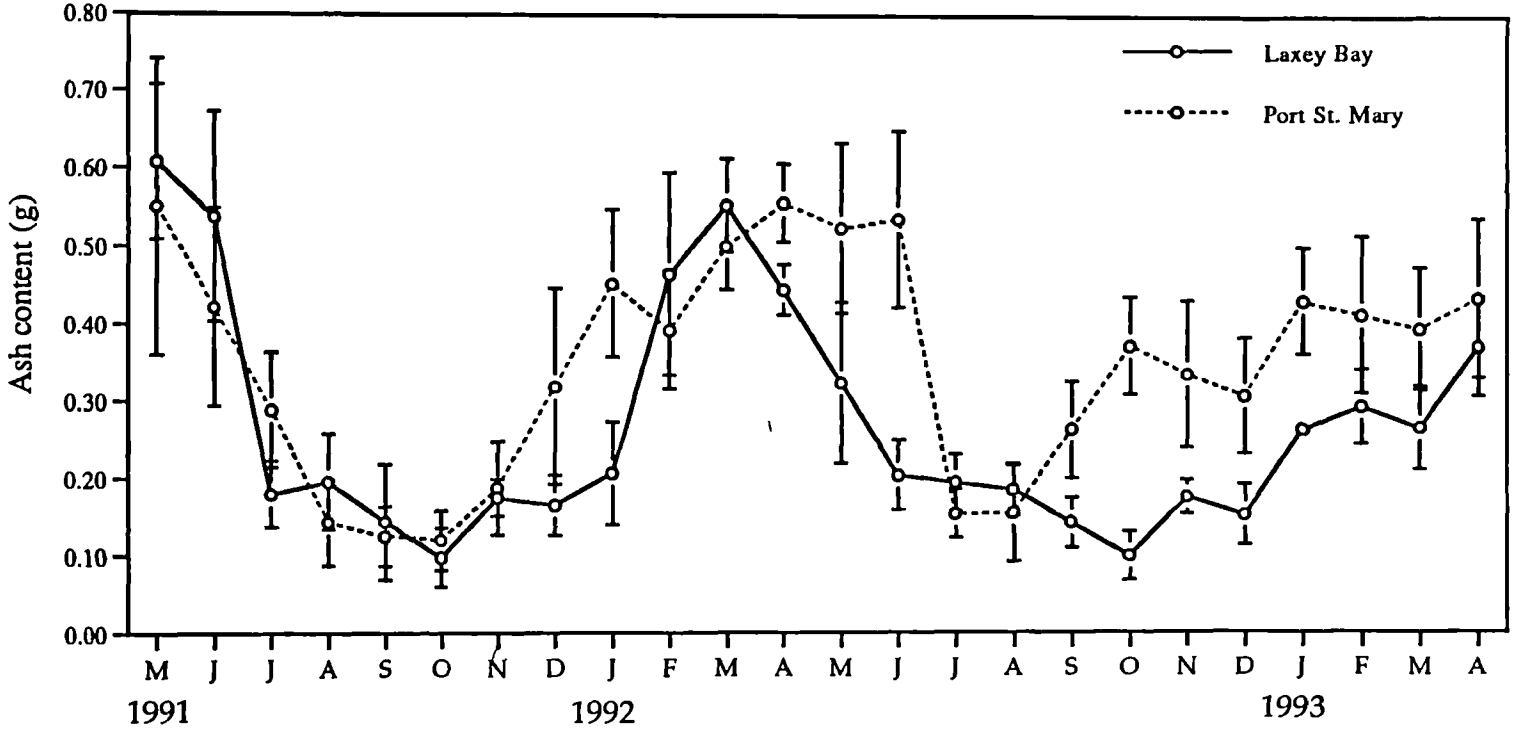


Fig. 3.38. Seasonal variation in the gonad (testis and ovary combined) ash content of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph.

recorded when the gonad was full. The ash weight was generally significantly higher ($p < 0.05$) in animals from the Port St. Mary ground, compared with Laxey Bay, in the autumn and winter months when the gonad was in better condition.

f. Water

The percentage of water in the gonads of *Pecten maximus* (Fig.3.39) varied similarly to the variation of gonad water in *A. opercularis* (Fig.3.15) during the two year period. It increased rapidly in summer to a high level in August - October, then fell steadily through the autumn, winter and spring. The amplitude of seasonal cycles was generally in the range 77% - 85% on both grounds. The monthly values were rather variable as indicated by the relatively high 95% confidence intervals (Fig.3.39) but there was evidence of two peaks in the year for the Laxey Bay population and a single earlier peak for the Port St. Mary population.

3.3.2.3 Mantle tissue

a. Protein

The seasonal fluctuations in the percentage of protein in the mantle tissue (Fig.3.40a) were less well-marked and with a rather different pattern to those in the adductor muscle (Fig.3.26a). For the mantle tissue there were two more or less distinct peaks and troughs each year on both grounds, instead of the single peaks found in adductor muscle. Protein levels were high in July and February and low in November- December and again in May-June. The values recorded were generally significantly higher ($p <$

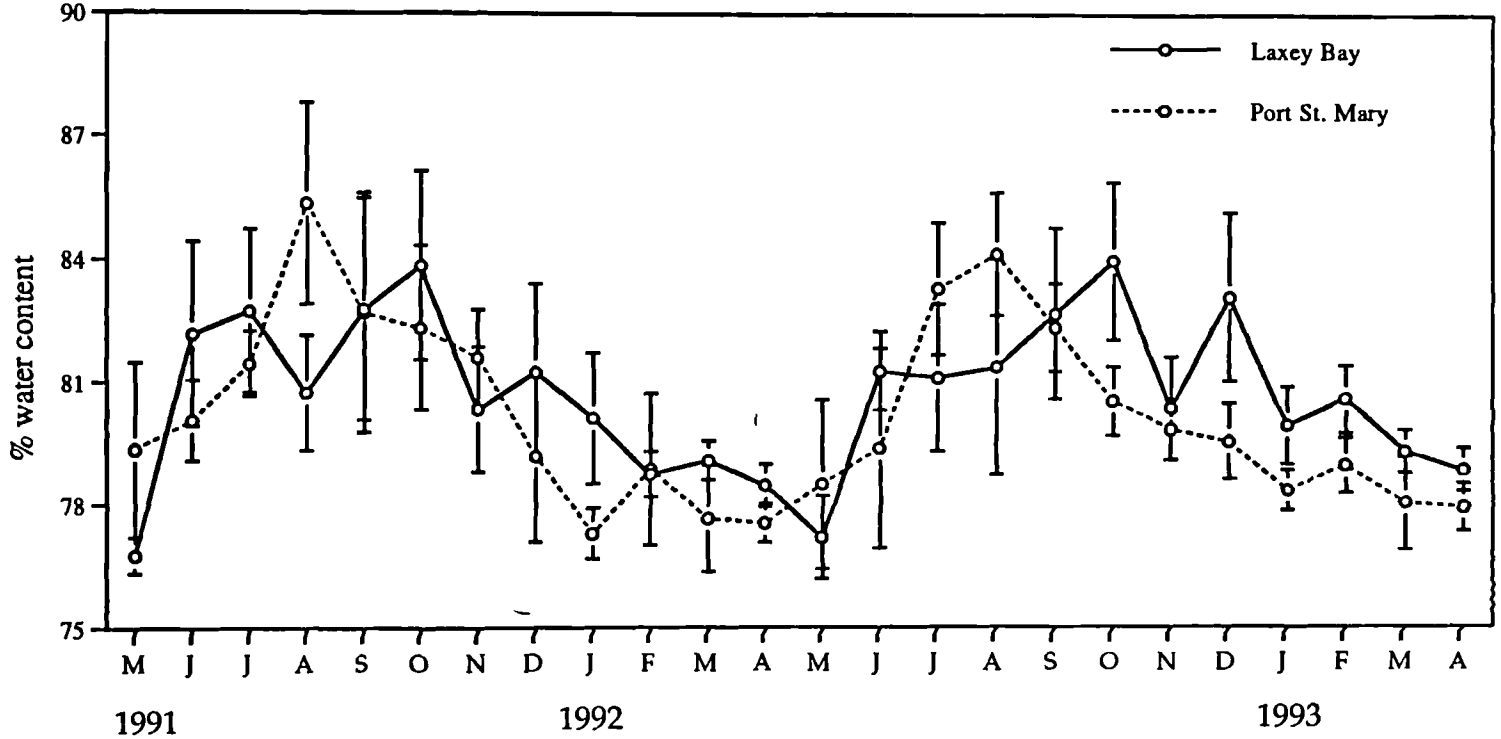


Fig. 3.39. Seasonal variation in the percentage water content of the gonad (testis and ovary combined) of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals.

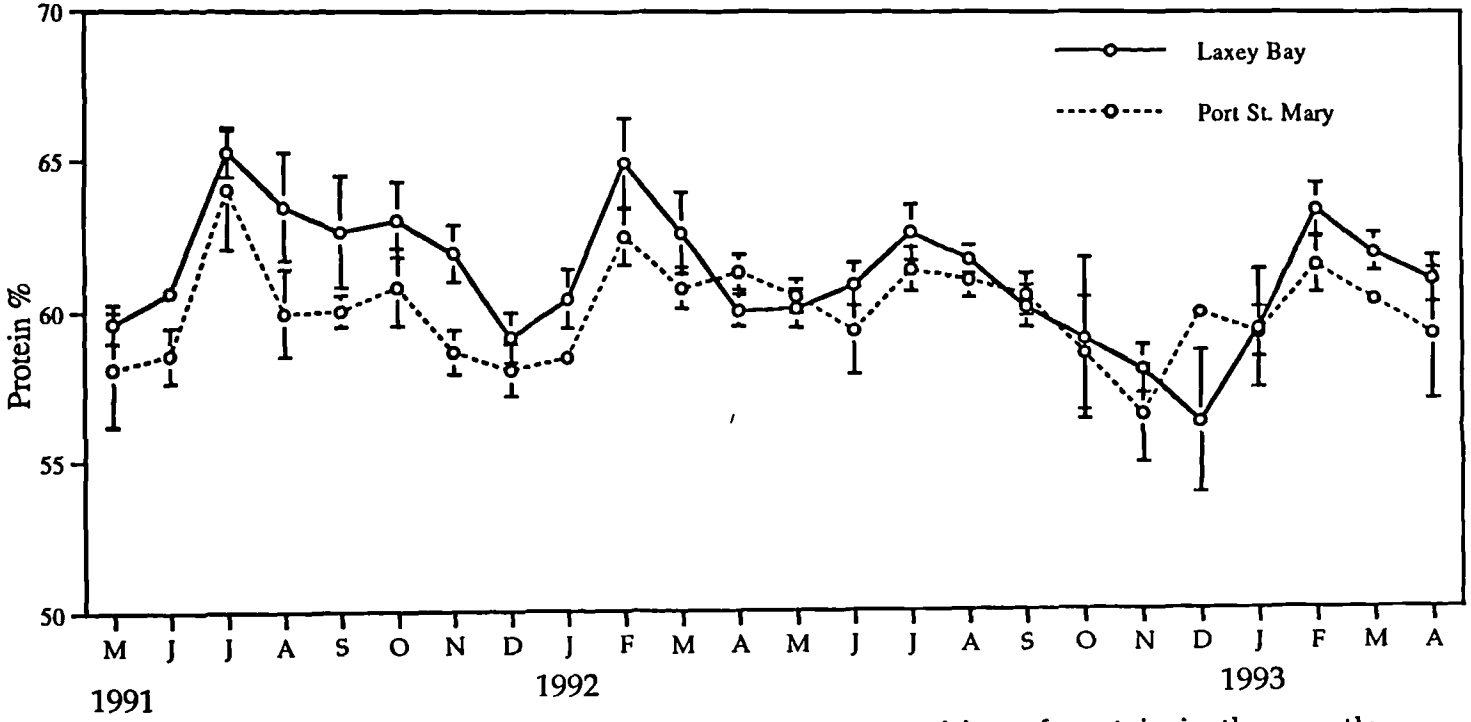


Fig. 3. 40a. Seasonal variation in the percentage composition of protein in the mantle tissue of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

0.05) for the Laxey Bay population compared with Port St. Mary, for the first year of study but thereafter there were no consistence differences.

The absolute content of protein (Fig. 3.40b) followed a similar seasonal pattern to the percentage changes but it was generally lower for the offshore Port St. Mary population, compared with the Laxey Bay population, throughout the study.

b. Lipid

The percentage lipid in the mantle tissue of both populations was at a low level, ranging from 2% - 4% over the two years (Fig. 3.41a). There was no clear variation but there appeared to be a general increase through the period of study.

The absolute lipid content of mantle tissue showed the same pattern (Fig.3.41b) rising to a higher level in 1992/93 than in the previous year. Lipid contents of the mantle tissue appeared to be generally higher in the inshore Laxey Bay population, than the offshore Port St. Mary population, throughout the study.

c. Glycogen

The percentage glycogen in mantle tissue was also at a relatively low level (0.5% - 4%) throughout the period of study (Fig.3. 42a). Apart from the one high value recorded for the Port St. Mary population in October 1991 it was generally at a higher level for most of the second year of study on both grounds.

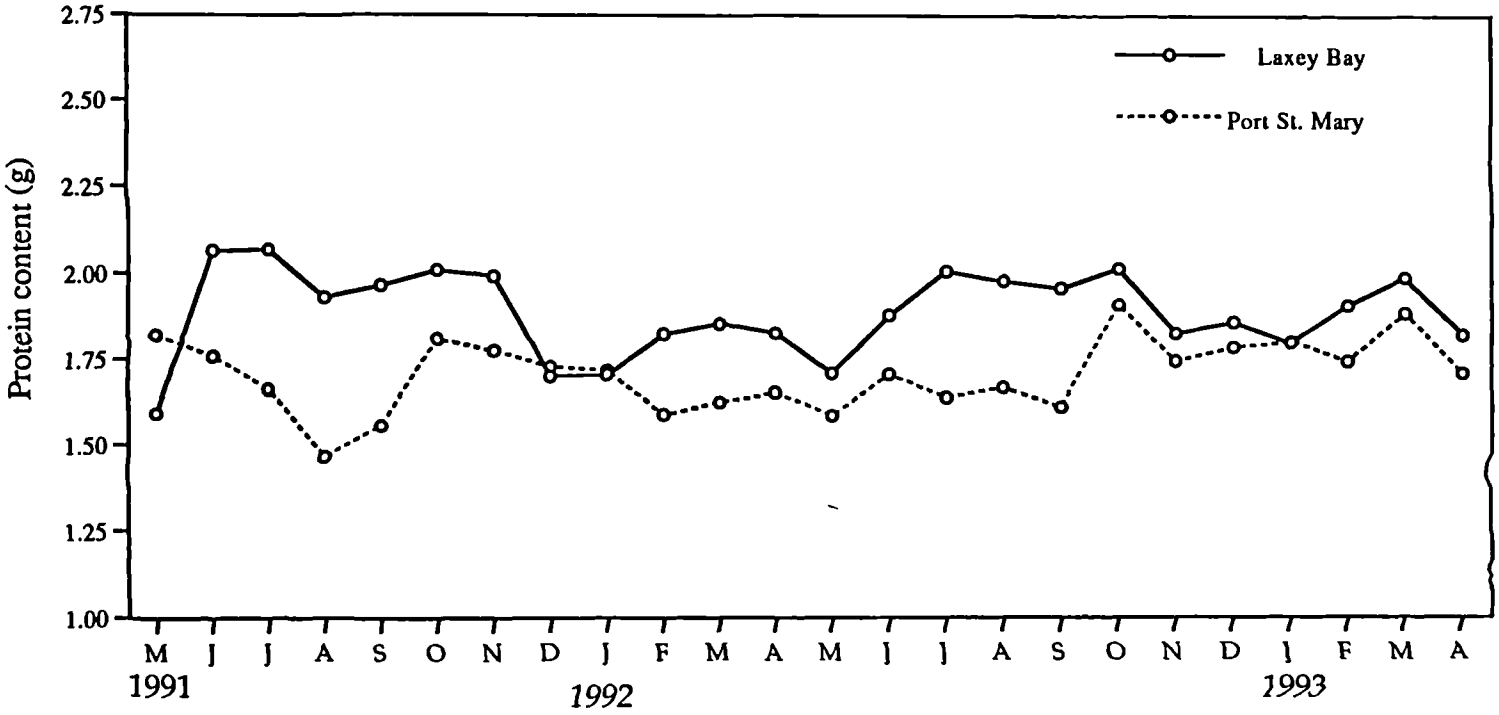


Fig. 3.40b. Seasonal variation in the protein content of the mantle tissue of *Pecten maximus* (125 - 130 mm length) from Laxey Bay and Port St. Mary (n = 10 - 15).

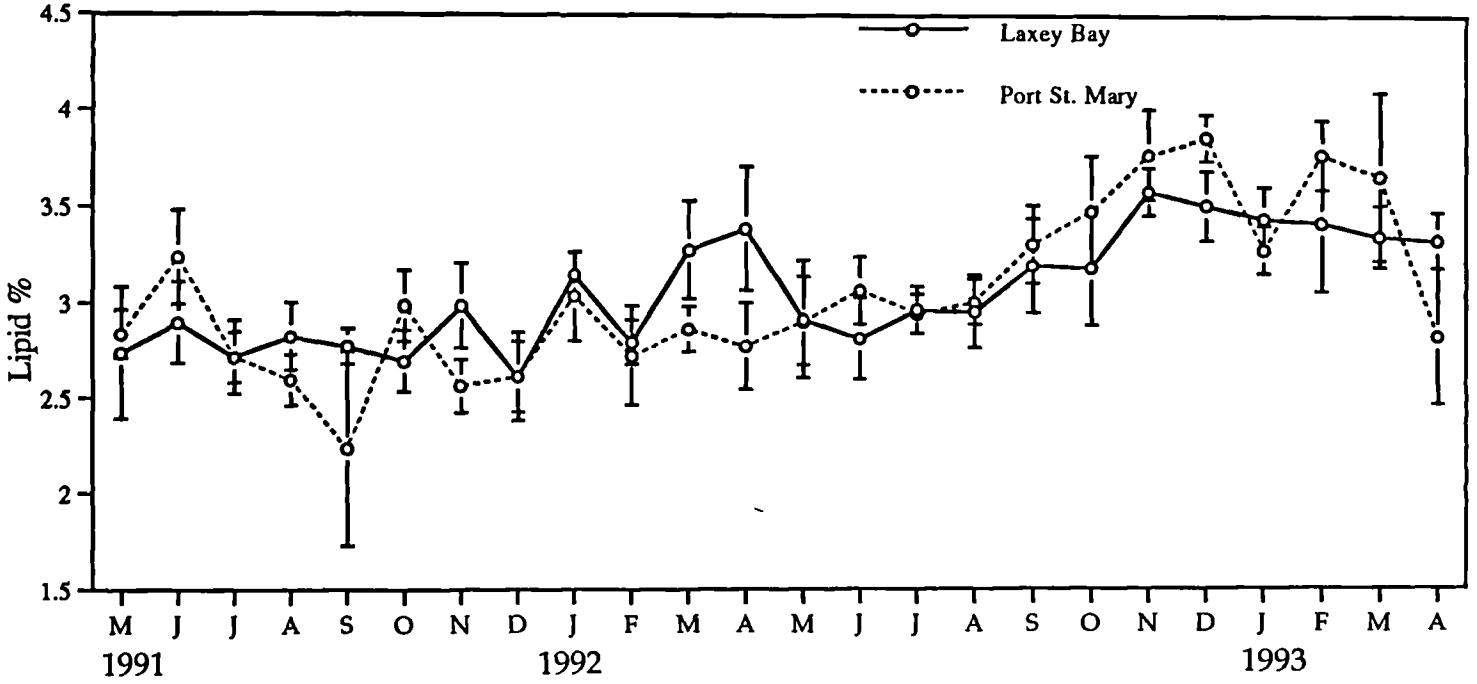


Fig. 3.41a. Seasonal variation in the percentage composition of lipid in the mantle tissue of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals (n = 10 - 15).

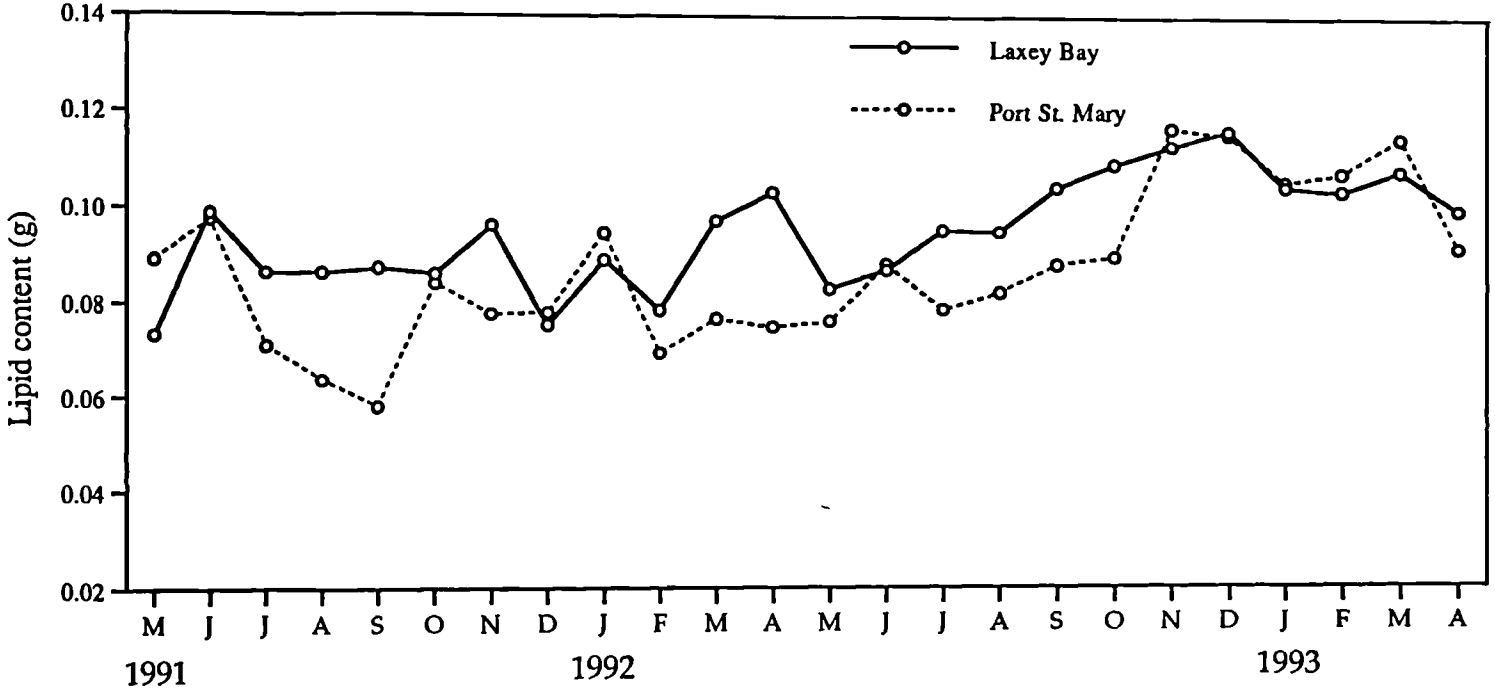


Fig . 3.41b. Seasonal variation in the lipid content of the mantle tissue of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary (n = 10 - 15).

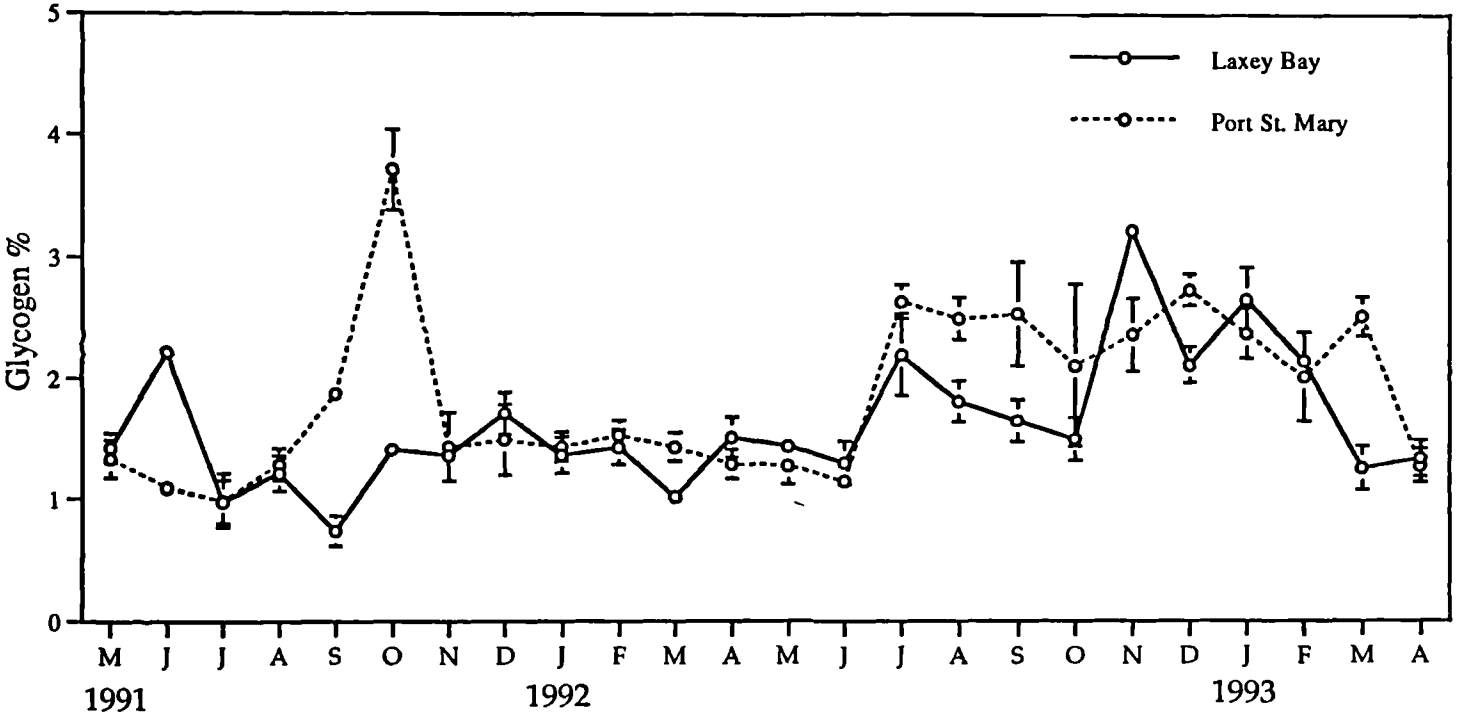


Fig. 3.42a. Seasonal variation in the percentage composition of glycogen in the mantle tissue of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

The absolute content of glycogen was also low, ranging from 0.03g - 0.12g, for both population during the two years (Fig. 3.42b), and followed the same pattern.

d. Water

As in the queen scallop *A. opercularis*, there is a large amount of body fluid in the mantle tissue of *P. maximus* so that the water content is very high, with monthly means ranging from 88% - 91% throughout the period of study (Fig. 3.43). Individual variation was high, as indicated by the high 95% confidence intervals so that no seasonal trends or differences between populations could be detected.

3.3.2.4 Digestive gland

a. Protein

The percentage of protein in the digestive gland of *P. maximus* showed a clear seasonal variation (Fig. 3.44a) and followed a similar cycle on both grounds. In 1991 it fell rapidly from July or August to a low level in November - December, then increased to its highest level in April - June 1992. In 1992 the rapid decline started earlier, from May (Laxey Bay) or June (Port St. Mary) and again continued until November - December before increasing rapidly in January and February 1993. Although the amplitude of the cycle was very similar in the two population there was some difference in the timing so that some of the monthly values were significantly different ($p < 0.05$). The Laxey Bay samples were generally lower than the Port St. Mary samples in 1991 but in 1992 and 1993 this

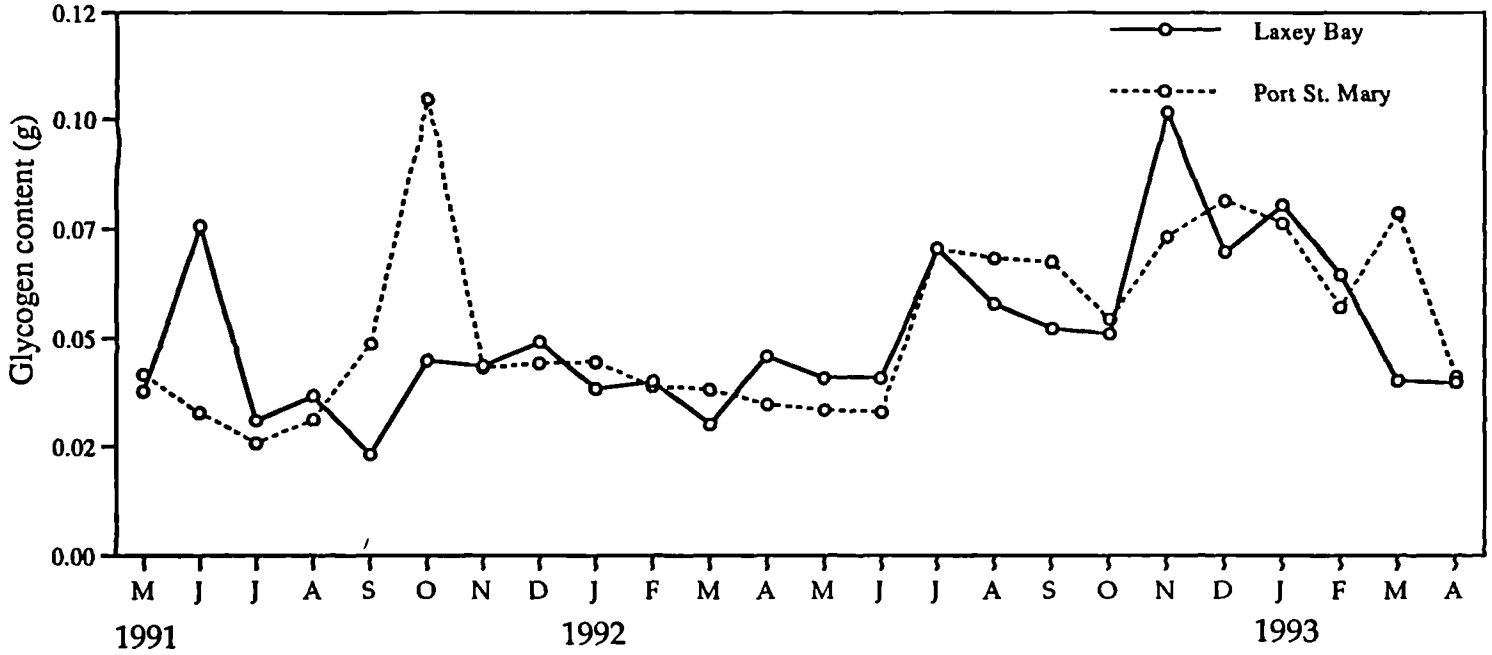


Fig. 3.42b. Seasonal variation in the glycogen content of the mantle tissue of *Pecten maximus* (120 - 130 mm shell lenght) from Laxey Bay and Port St. Mary (n = 10 - 15).

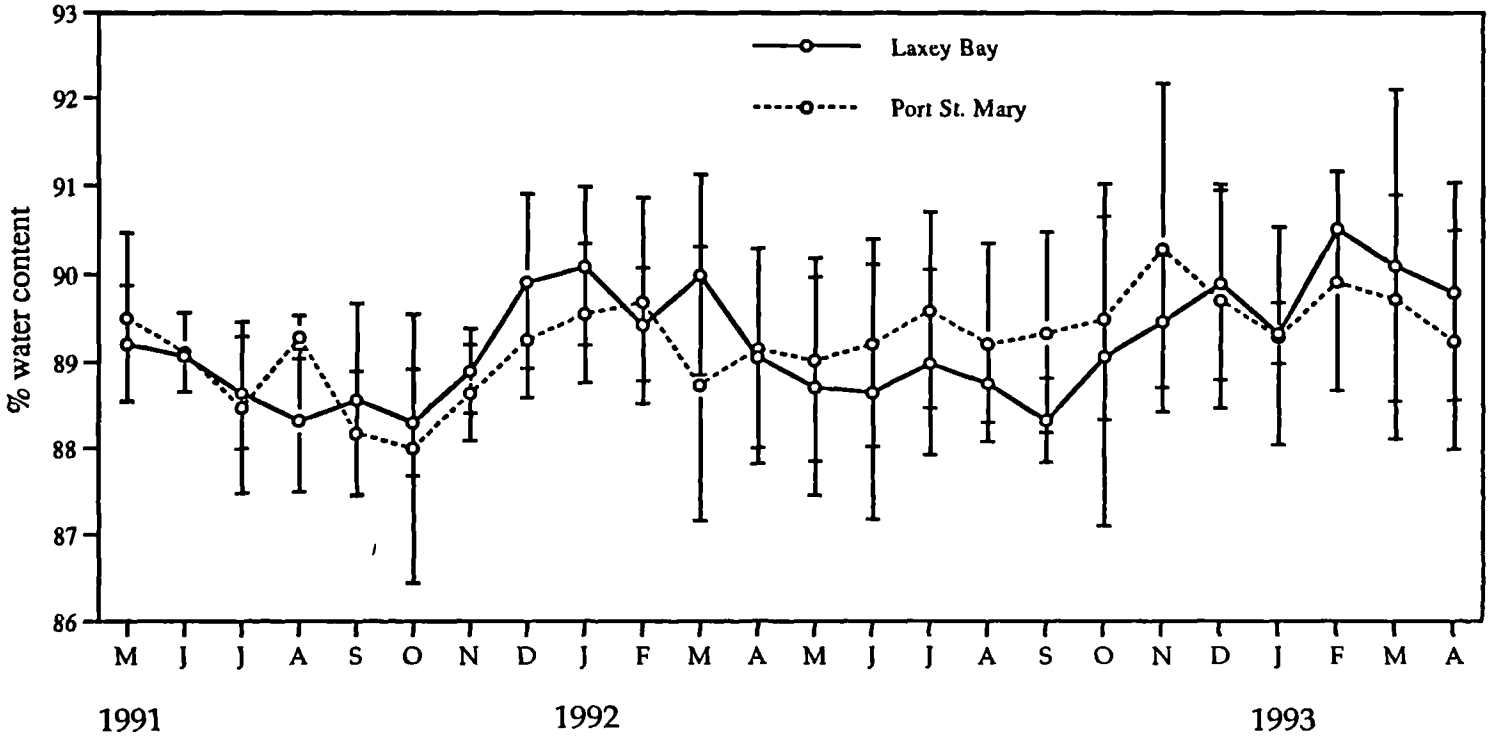


Fig. 3.43. Seasonal variation in the percentage water content of mantle tissue of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals.

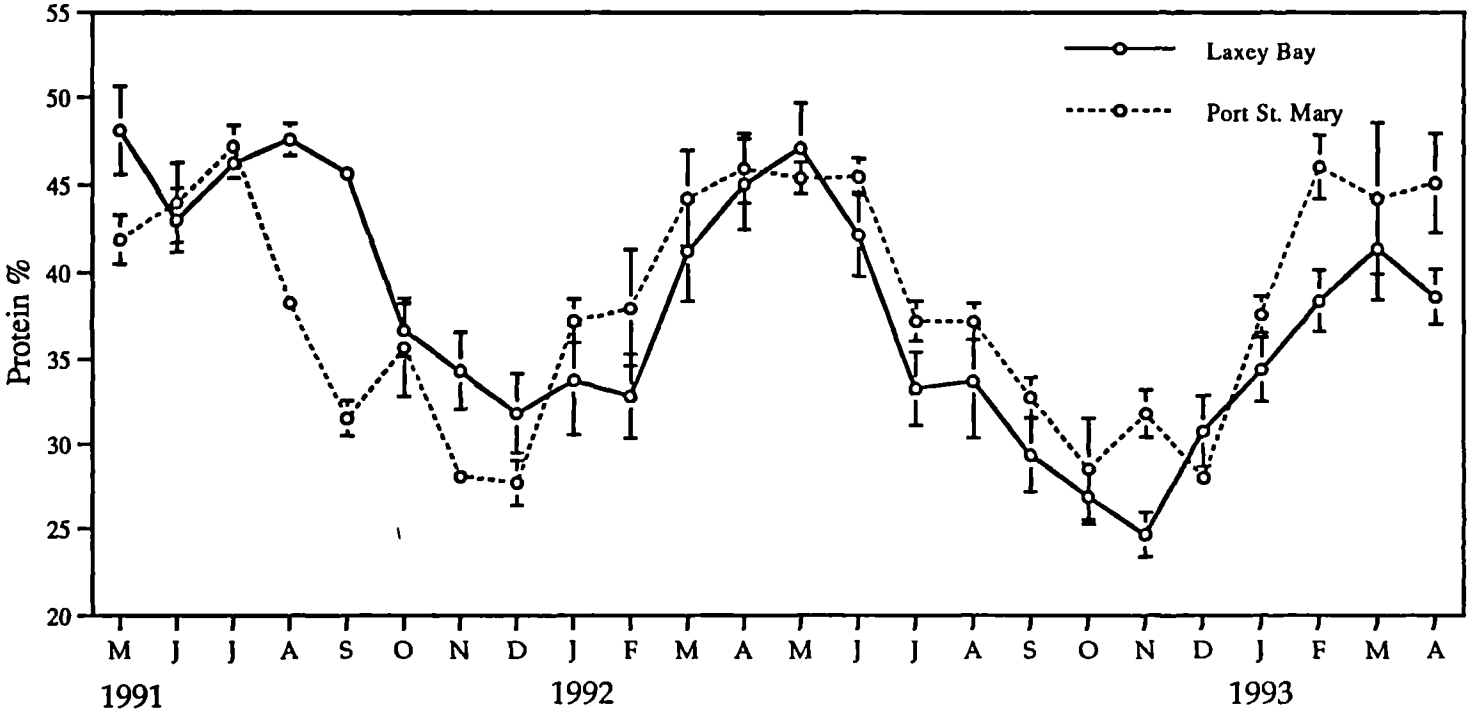


Fig. 3.44a. Seasonal variation in the percentage composition of protein in the digestive gland of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

position was reversed. Protein levels were generally rather low in the digestive gland (24% - 48%) compared to other tissues of the animal.

The absolute content of protein in animals of mean size (Fig. 3.44b) also showed clear seasonal cycles, particularly on the offshore Port St. Mary ground where it built up to a much higher peak than the Laxey Bay population in July and August, then fell to a low level in the period November - March.

b. Lipid

The percentage of lipid in the digestive gland (Fig. 3.45a) was much higher than in any other tissue and had a very clear seasonal cycle. It increased to a maximum in late summer and early autumn, then fell rapidly to a low level in winter and early spring. There were, however, some differences in timing and amplitude between the two populations. In 1991, the percentage lipid in the Laxey Bay population showed a small but significant ($p < 0.05$) fall between June and July, then rose rapidly to a high peak in October before falling rapidly to its lowest level in December. In contrast, lipid levels in the offshore Port St. Mary population increased steadily to a lower and later maximum in December, before falling sharply in January. In 1992 the pattern was similar but lipid levels in both populations built-up more quickly in early summer and remained at a high level until February or March 1993.

The absolute content of lipid followed a similar seasonal pattern to the percentage changes throughout the period of study (Fig. 3.45b). However, lipid content of Port St. Mary scallops built-up much more rapidly and reached its maximum some 2-3 months earlier than the Laxey Bay scallops

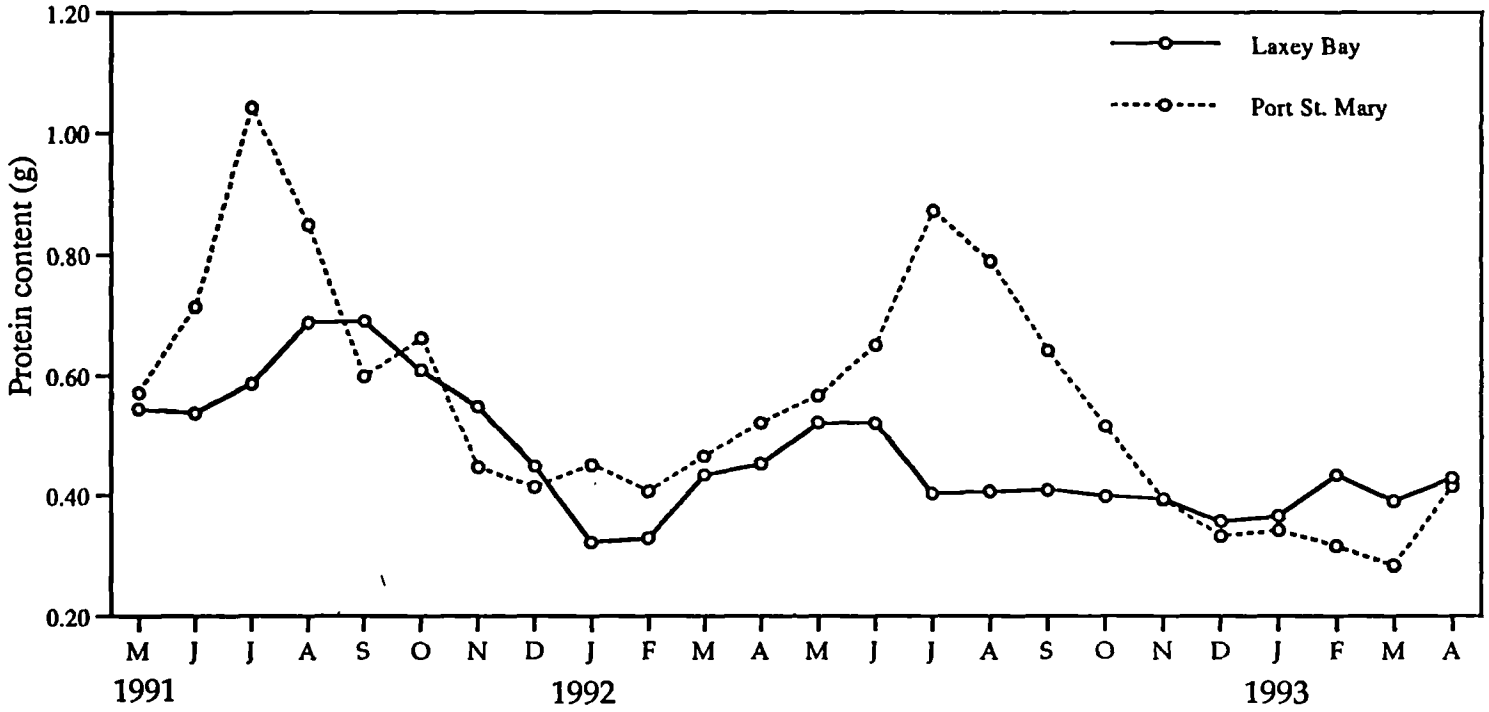


Fig. 3.44b. Seasonal variation in the protein content of the digestive gland of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary (n = 10 - 15).

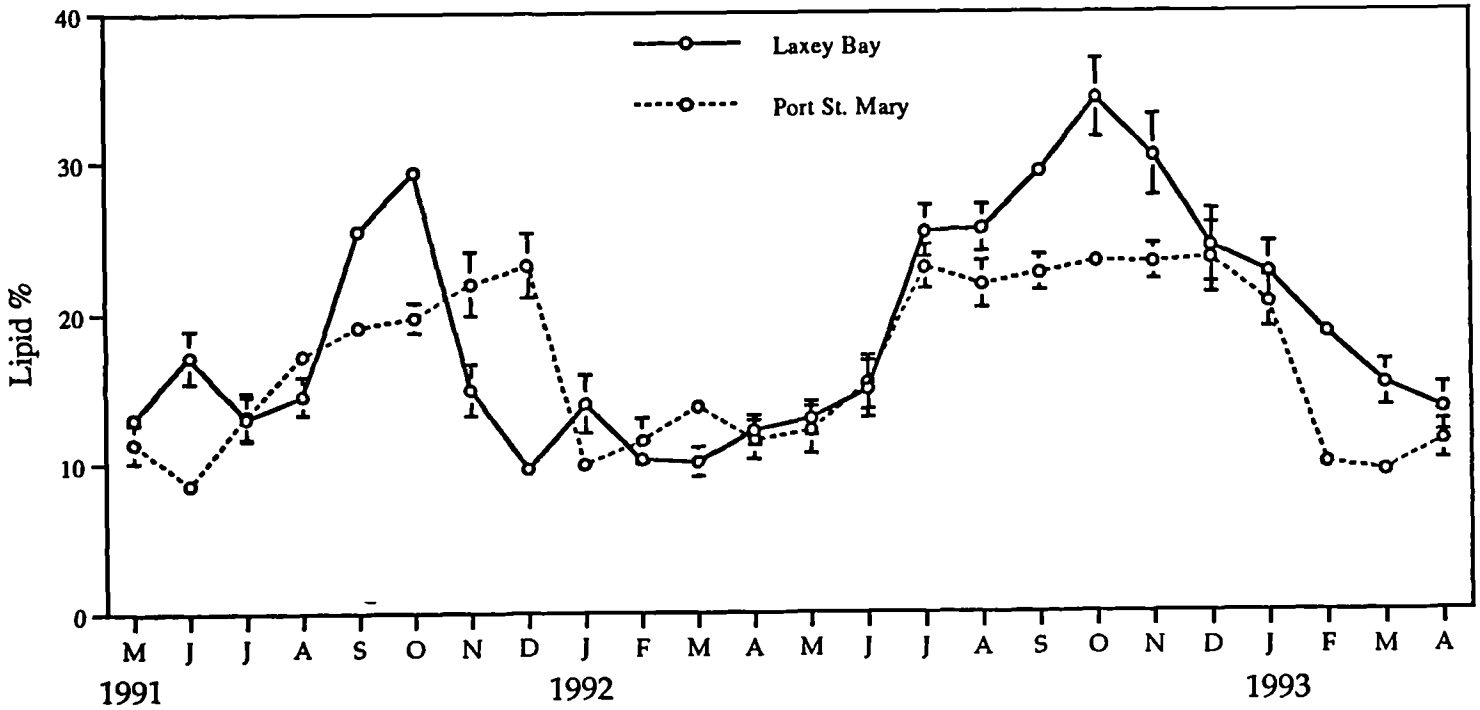


Fig. 3.45a. Seasonal variation in the percentage compositon of lipid in the digestive gland of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

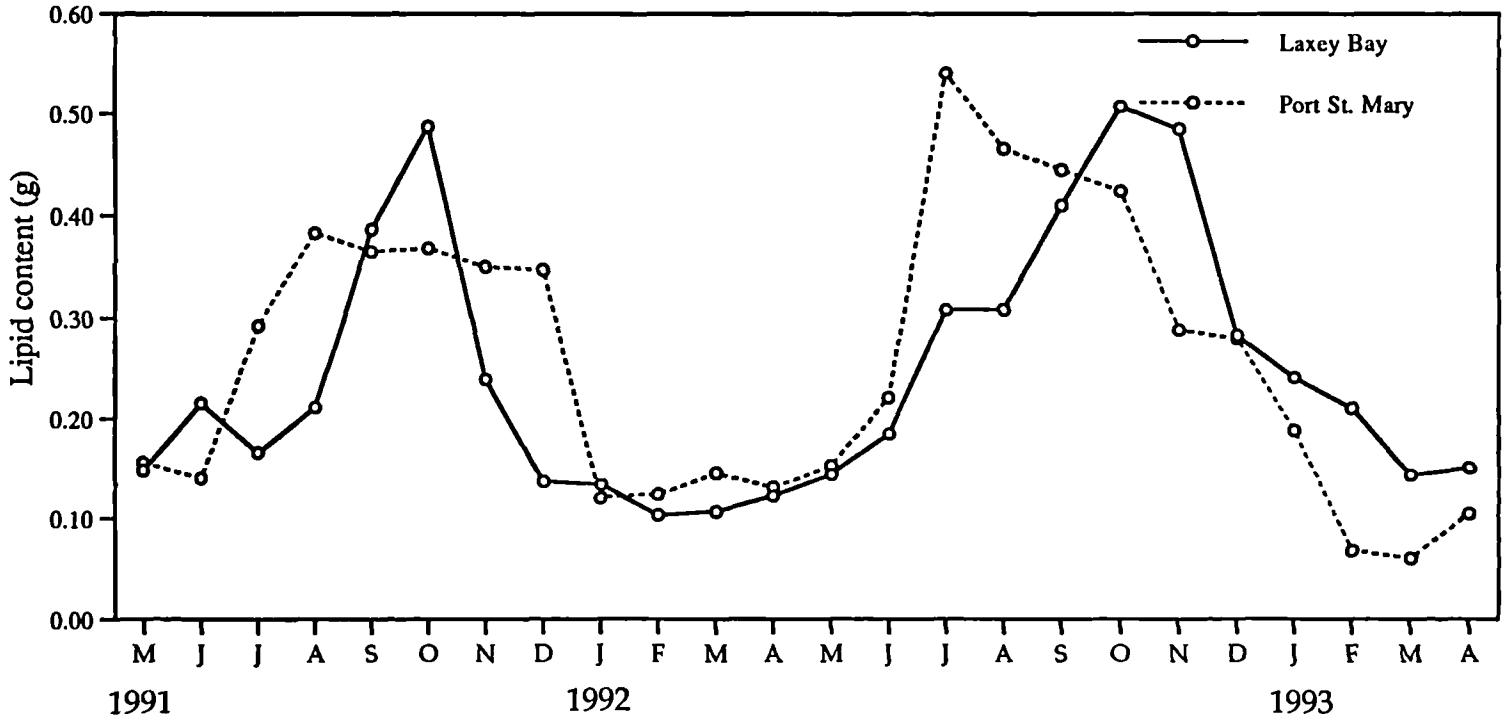


Fig. 3.45b. Seasonal variation in the lipid content of the digestive gland of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary (n = 10 - 15).

in both years. In 1992 the maximum lipid contents attained was actually higher in Port St. Mary scallops, despite the very high percentage composition of the Laxey Bay population.

c. Glycogen

The percentage of glycogen in the digestive gland (Fig. 3.46a) showed no clear seasonal variation in the two populations. The pattern of change was more erratic and varied over a greater range in the Port St. Mary population, compared with the Laxey Bay population. The levels of glycogen recorded were significantly higher ($p < 0.05$) in the Port St. Mary population during the period July - November 1992, but although many of the other monthly values recorded were significantly different between the two grounds, there was no consistent pattern.

The absolute content of glycogen (Fig. 3.46b) showed a more obvious pattern, which differed for the two grounds. For the Laxey Bay population seasonal fluctuations were small, building up slowly to the highest levels in autumn and falling to the lowest in Februay or March. In contrast, the seasonal cycle in the Port St. Mary population was much earlier and much greater in amplitude, rising sharply to a peak in July before falling to a minimum in February.

d. Ash

The ash content calculated was a combination of mantle tissue, gill, and digestive gland (Fig. 3.47). Individual variability was high so that, apart from May and June 1991, when ash weight was significantly higher ($p <$

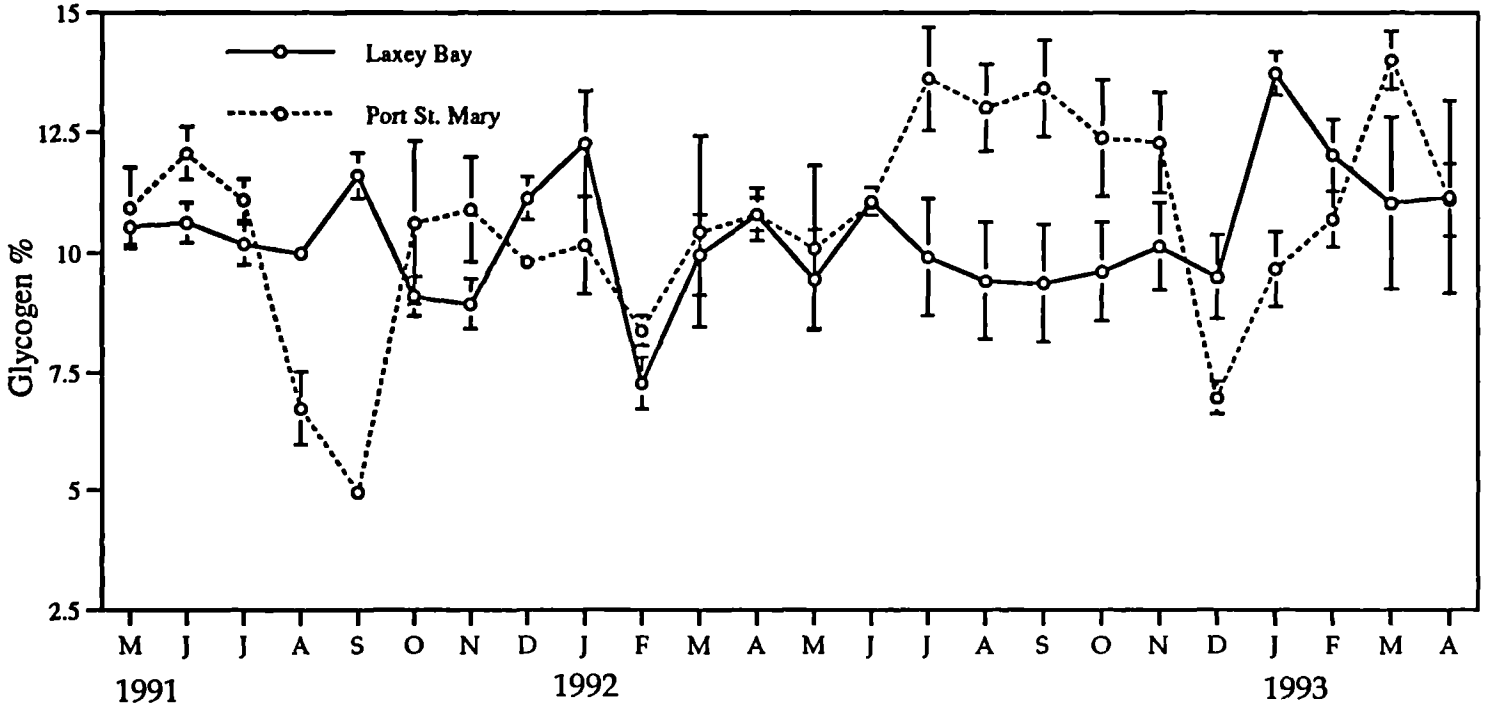


Fig. 3.46a. Seasonal variation in the percentage composition of glycogen in the digestive gland of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals. Error bars smaller than data points do not appear on the graph (n = 10 - 15).

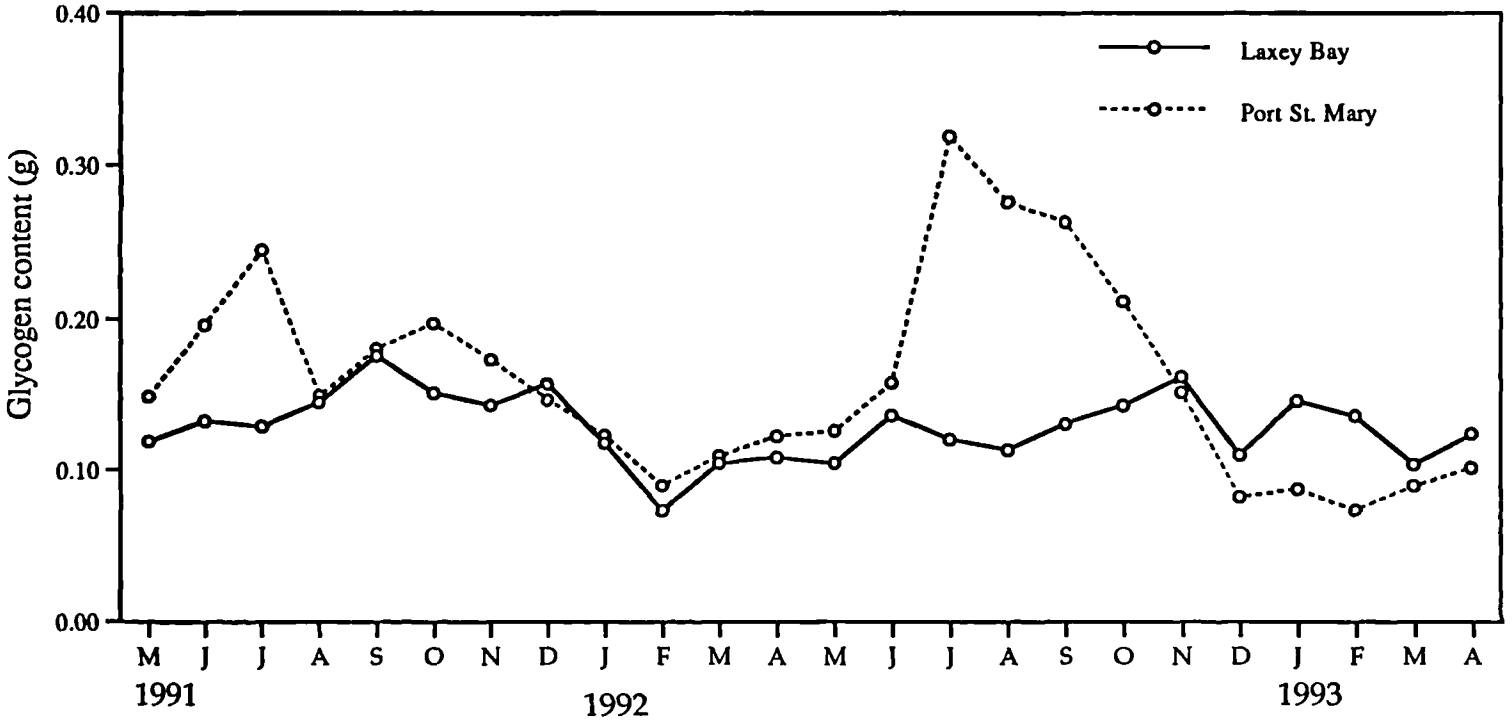


Fig. 3.46b. Seasonal variation in the glycogen content of the digestive gland of *Pecten maximus* (120 - 130 mm shell lenth) from Laxey Bay and Port St. Mary (n = 10 - 15).

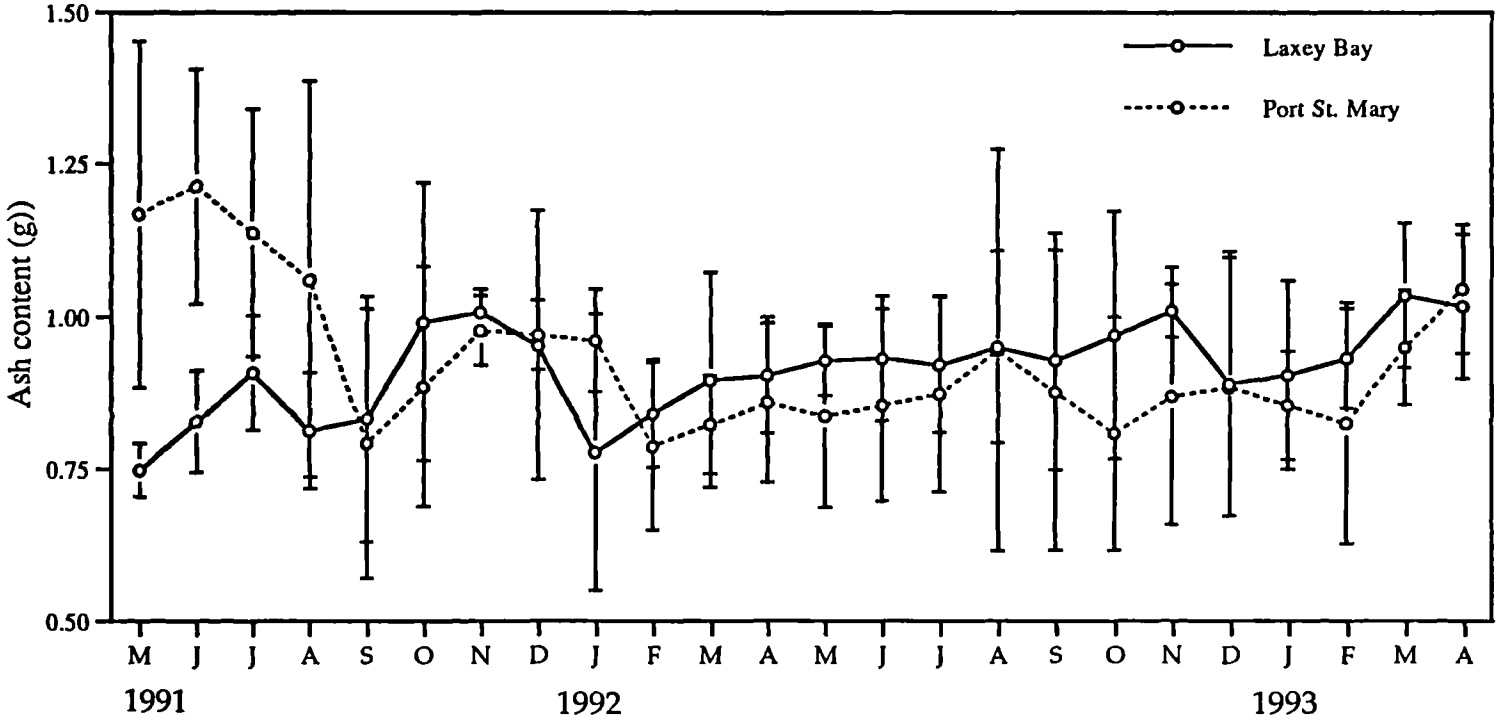


Fig. 3.47. Seasonal variation in 'other tissues' (mantle tissue, gill, digestive gland combined) ash weight of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals.

0.05) for the offshore Port St. Mary population, there was no difference between the two populations and no apparent seasonal trends. The percentage ash varied from 17% - 26% for the two populations.

e. Water

The variation of percentage water in the digestive gland (Fig. 3.48) followed a similar pattern to that in the adductor muscle (Fig. 3. 30). The seasonal cycle was very similar in amplitude and timing on the two grounds, being generally highest in March - April and lowest in September. Seasonal fluctuations of water content were about 10% on both grounds during the sampling period and the values recorded for the digestive gland were low compared with other tissues in the animals.

3.3.2.5 Percentage of total water

The total tissue water content also underwent a similar seasonal variation to that indicated by the adductor muscle, mantle tissue and digestive gland (Fig. 3.49). The percentage water content of *P.maximus* from Laxey Bay varied from 80.83% to 83.64%, while during the same period animals from Port St. Mary varied from 79.41% to 83.50%. The values recorded for the Laxey Bay population were higher ($p < 0.05$) than the Port St. Mary population in October 1991 and in March 1992 but otherwise there were no statistically significant differences.

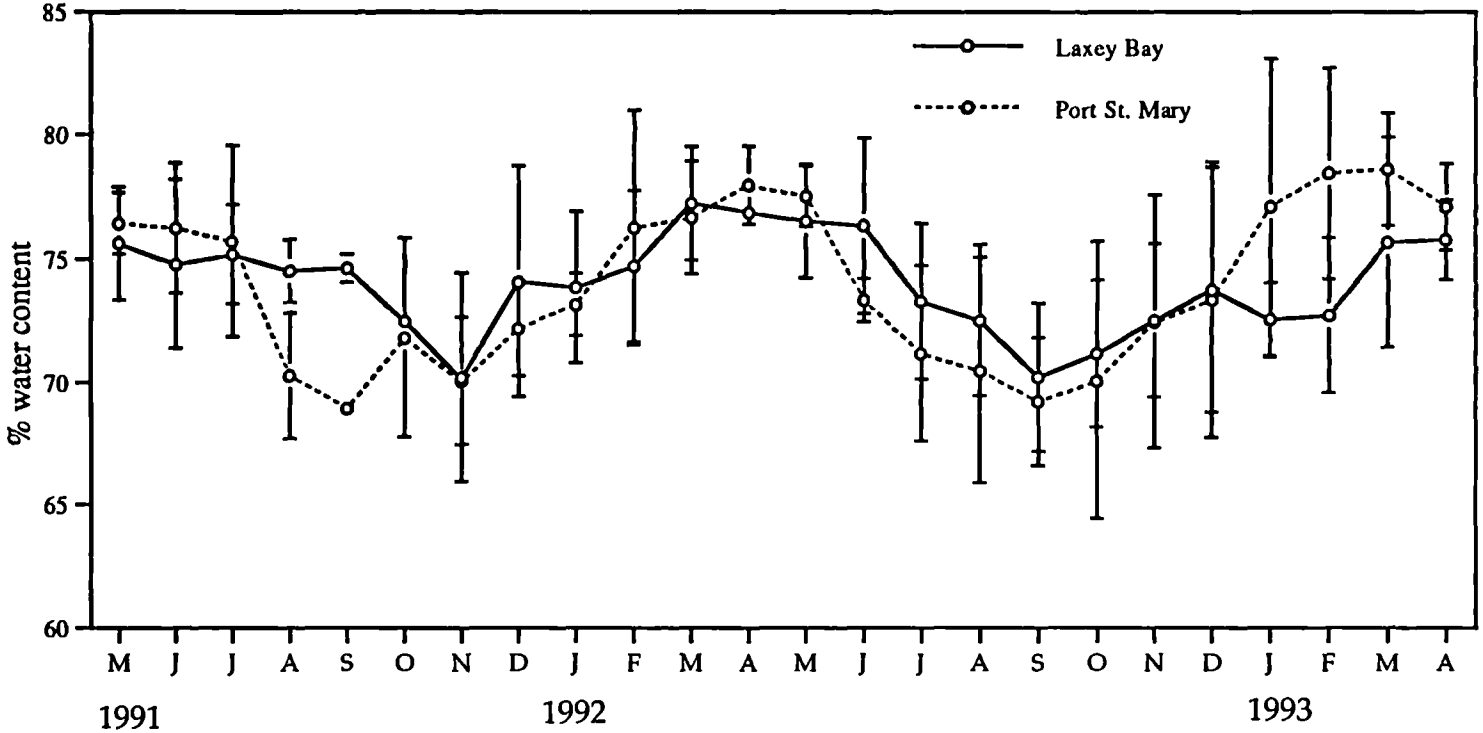


Fig. 3.48. Seasonal variation in the percentage water content of the digestive gland of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals.

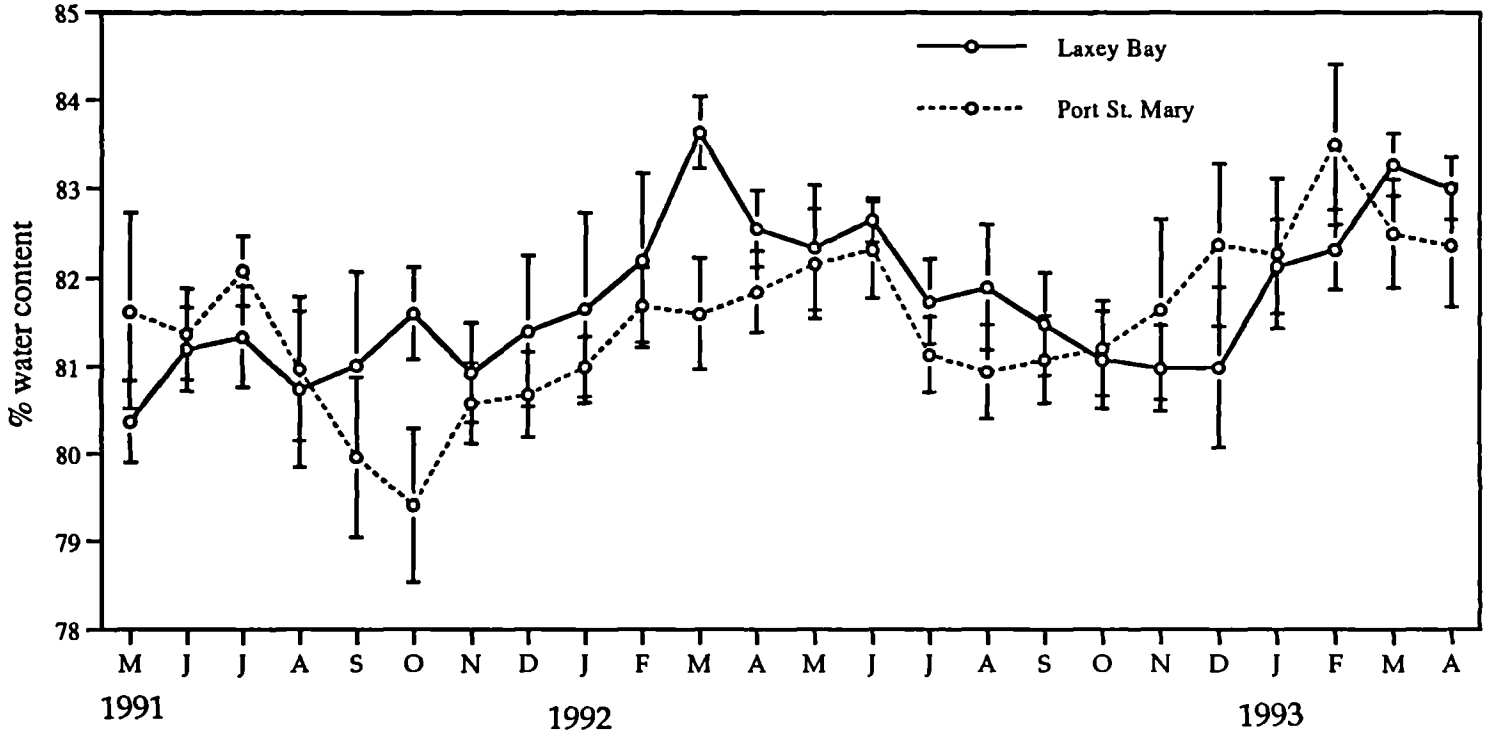


Fig. 3.49. Seasonal variation in the percentage water content of the total tissue of *Pecten maximus* (120 - 130 mm shell length) from Laxey Bay and Port St. Mary. Values represent means and 95% confidence intervals.

3.4 DISCUSSION

In general, the chemical estimation of protein, lipid and glycogen is straightforward, using standard techniques, but the presentation and interpretation of results can be problematical. Two methods of presentation are commonly used. Each biochemical component may be expressed according to the percentage composition in the dry weight of the sample or it may expressed as the actual weight of that component in an individual animal. The percentage composition takes account of body weight differences between individual animals but it suffers from the inherent problem of proportions in that changes in one component can arise from reciprocal variations in the other components. Thus, the actual weight or content of each component in an individual animal or tissue is often more meaningful, but to allow comparisons to be made this must be estimated for an animal of a restricted size range (or calculated for a standard size animal)

In the present study both methods of presentation were employed in order to aid the interpretation of seasonal events. For some tissues, such as the adductor muscles, where there were large seasonal fluctuations of protein and glycogen in both species, the seasonal patterns of change illustrated by the two methods of presentation were very different in timing, which highlights the problem of interpreting seasonal cycles from % composition data. In addition, where a particular biochemical component was not well-represented in a tissue, such as lipid in the adductor muscle and the testis, no clear seasonal pattern was apparent from the % composition data but a very clear cycle was evident in the absolute content data.

The biochemical composition of the various tissue components of *A. opercularis* and *P. maximus* on the two fishing grounds showed a complex

series of seasonal cycles over the two years of the study. In general, protein, lipid and glycogen were stored in the adductor muscle, mantle and digestive gland in the spring and summer, when food was abundant, and these energy reserves were subsequently utilized for maintenance or in the production of gametes during autumn and winter. The seasonal changes in biochemical content were generally much greater in the adductor and gonad, than in the other tissues. Such a cycle of energy storage and utilization has been previously described for various species of scallops (Ansell, 1974a, b, c; Comely, 1974; Taylor & Venn, 1979; Sundet & Vahl, 1981; Barber & Blake, 1981, 1991) and other bivalves (Establier, 1969; Adachi, 1979; Holland, 1978). The importance of substrates, composition of stored reserves, where in the animal they are stored and the timing of utilization, varies with the species (Giese, 1969; Sastry, 1979).

In the present study of the biochemical composition of tissues of *A. opercularis* and *P. maximus*, in Manx waters, protein made up the largest proportion throughout the two years in all tissues, as previously noted in these species of scallops (Comely, 1974; Taylor & Venn, 1979; Mackie, 1986) and in other bivalves (Giese *et al.*, 1967, Giese, 1969).

Protein is a major cellular structural material in all tissues but under certain conditions it has been found to be an important source of energy (Giese, 1966, Giese *et al.*, 1967). Thus, Gabbott & Bayne (1973) noted that during starvation, *Mytilus edulis* utilised reserves of protein to carry out metabolic activities and Sundet & Vahl (1981) found that the Iceland scallop, *Chlamys islandica*, utilised body protein as an energy source during the winter months.

Protein has been shown to constitute the major organic component of oocytes of two populations of the bivalve *Venerupis japonica* (Holland, 1978) and gonadal protein has been observed to increase while the adductor muscle protein decreased in a number of marine bivalve species (Establier, 1969; Williams, 1969; Ansell, 1972, 1974; Beukema & Bruin, 1977; Nagabhushanam & Talikhedar, 1977; Ansell *et al.*, 1980). Establier (1969), Comely (1974) and Holland (1978) suggested that, for various bivalves, nitrogenous reserves provide the material for gametogenesis while glycogen supplies the main metabolic substrate. However, in *Argopecten irradians concentricus*, adductor muscle glycogen is utilised primarily for oogenesis and protein is used to meet maintenance requirements during the later stage of oogenesis and spawning at a time when food is becoming less abundant (Sastry, 1968; Barber and Blake, 1981).

The results of the present study indicate that the loss of protein in the adductor muscle of *A. opercularis* and *P. maximus* during the winter was coincident with the increase in the weight of protein in the gonads, as found in previous studies of other scallop species (Sastry, 1979; Barber & Blake, 1981).

However, the increase in weight of protein in the gonads did not account fully for the loss in the weight of protein from the adductor muscle, particularly in *A. opercularis*. Furthermore, protein contents in the mantle tissues of both *A. opercularis* and *P. maximus* followed a similar seasonal pattern to the protein of the adductor muscle, though the seasonal fluctuations were of a lower magnitude, and there were further small decreases in protein in the digestive gland. Taken together, these decreases in protein more than compensated for the increase in protein in the gonads in both species and strongly suggest that protein from these various tissues

is contributing to general maintenance energy requirements in the winter months. Faveris & Lubet (1991) have also suggested that the mantle tissue contributed energy during gametogenesis of *P. maximus* in the Baie De Seine.

The build-up of protein in the ovary and in the testis followed a slightly different pattern during gametogenesis in both species, indicating a different time requirement for the build-up of sperm and ovary. As observed by Mackie (1986) the build-up of protein was more rapid in the male than in the female gonad of *P. maximus* in the beginning of gametogenesis. The protein in the testis increased with the size of the testis during the winter and through spring, then decreased sharply after spawning in both *A. opercularis* and *P. maximus*. Depletion of protein from the gonads was presumably due to release of reproductive tissues into the environment. The protein content of the gonad was at a minimum in both species after spawning.

The protein content in the testis of both species was high compared with the ovaries throughout the period. Comely (1974) and Mackie (1986) also found significantly higher protein in the testis, compared with the ovary, in *P. maximus* in the Clyde Sea area and in Loch Creran. However, Lubet *et al* (1987) observed that the protein content was identical in the testis and the ovary of *P. maximus* in French waters. Similar differences have been recorded for other species. Thus, Thompson (1977) found higher protein levels in maturing and ripe testes than in the ovaries of the giant scallop, *Placopecten magellanicus,* from Newfoundland while Couturier & Newkirk (1991) found them to be nearly identical for the same species held in suspended culture.

In addition to protein, the ovaries accumulated considerable quantities of lipid during gametogenesis, while at the same time lipid contents fell in the digestive gland. A similar pattern during gametogenesis has been described for *Chlamys hericia* (Vassallo, 1973), *Argopecten irradians concentricus* (Barber & Blake, 1981) and *Placopecten magellanicus* (Couturier & Newkirk, 1991).

The digestive gland of both *A. opercularis* and *P. maximus* was observed to have a high content of lipid during the study, which built-up rapidly during the spring when phytoplankton levels are high. Scallops rely mainly on suspended detrital material and phytoplankton as their food resources (Bricelj & Shumway, 1991). Lawrence (1993) found many diatoms and dinoflagellates in the stomach of *A. opercularis* and *P. maximus* as a major food source. Therefore it is possible for them to store lipid in the digestive gland from lipid-rich phytoplankton (Schmidt-Nielson, 1975). High amounts of fatty acids were found in some diatoms and dinoflagellates, which are the main food resources of *Chlamys tehuelcha* (Sargent, 1976; Pollero *et al.*, 1979) and seasonal fatty acid changes in the somatic tissues and gonads of this species have been related to the fatty acid composition of the phytoplankton (Pollero *et al.*, 1979). In contrast, Watanabe & Acman (1974) and Lewin *et al.*, (1979) observed that bivalve fatty acid compositions in body components are species oriented rather than diet dependent, indicating that active fatty acid metabolism occurs (Lewin *et al.*, 1979).

For both scallops and queens the fall in lipid contents in the digestive gland during the period of gametogenesis, plus a smaller contribution from the adductor muscle, appeared to be more than adequate in weight to account for the lipid increase in the ovary but this does not preclude the possibility that the synthesis of certain fatty acids takes place from other substrates.

The percentage and the content of glycogen in the adductor muscle and digestive gland of both species observed in this study decreased from late autumn to early spring but this did not lead to an increase in glycogen in any other tissue of the animal, indicating that this was either used for maintenance or converted into another form of nutrient before use. Hatanaka (1940) and Tanaka & Hatano (1952) observed the conversion of glycogen into lipid by the Japanese oyster, *Crassostrea gigas* during gametogenesis. Gabbott (1975) and Beninger & Lucas (1984) also assumed the conversion of glycogen into lipid for gametogenesis and Martin (1961) and Giese (1966) considered that most of the lipids in pectinids were synthesised from other reserves to meet their requirements during periods of low food availability. Lipids serve as an energy reserve in adult bivalves especially during periods of nutritional insufficiency such as in winter conditions in temperate waters (Walne, 1970; Beukema & De Bruin, 1977).

Lipid stored in the gonad, especially in the ovary, plays an important role in bivalve physiology (Giese, 1966; Beninger & Lucas, 1984). Oocyte lipids are considered to be involved primarily in supplying the energetic requirements of the early larval stages (Gabbott, 1975; Holland, 1978).

The lipid content is highest in the digestive gland, perhaps because of its function as a site for lipid storage and utilization (Nakazima, 1956; Giese, 1966; Wilber & Yonge, 1966; Owen, 1966; Sastry, 1979). It has been identified as the most enzymically (lipase enzyme) active area of the alimentary canal, indicating that this is the main area of lipid synthesis and degradation (Patton & Quinn, 1973; Stark & Walker, 1983).

Gabbott & Bayne (1973) observed a group of *Mytilus edulis* starved during the winter and found that lipids contributed 15% of the maintenance energy

and glycogen contributed 10%. Beninger & Lucas (1984) noted that lipid may provide up to twice as much reserve energy as glycogen under prolonged and severe situations of energy imbalance. Holland & Hannant (1973) and Beninger & Lucas (1984) have noted that the precise role of lipids as an energy reserve in adult bivalves remains to be cleared-up, particularly that of the large phospholipid fraction.

For studies relating to reproductive energy metabolism, tracing radio-active labelled compounds can provide more direct information with respect to the movement of particular substrates within the animal. Sastry and Blake (1971) have found that direct transfer of ^{14}C-leucine from the digestive gland to the gonad in *Argopecten irradians* is associated with the initiation of oocyte development. Vassallo (1973) observed that when ^{14}C- lipid *Chlorella* extract was fed to *Chlamys hericia*, gonadal lipid activity increased as digestive lipid activity decreased. These and other radiotracer experiments (Sastry & Blake, 1971; Vassallo, 1973; Barber & Blake, 1985) support the present results in which the lipid in the digestive gland of both species showed inverse relationships with those in the ovary during gametogenesis, indicating that the lipid may be transferred directly from the digestive gland to the developing ova. The results indicated that a gradual increase in gonadal lipid of both species over the late autumn and winter was then followed by a rapid increase in lipid prior to spawning. This may be a result of the increase of phytoplankton levels in late spring in the Irish Sea (see, General Discussion).

Early phytoplankton blooms have been considered to be necessary for oocyte maturity in various *P. maximus* populations (Mackie, 1986; Lubet *et al.*, 1987). For *Chlamys varia*, gametogenesis started with the maximum availability of food (Burnell, 1983). In *A. opercularis* kept in cages at

Portmouth on the English Channel three spawnings were found to be related to the abundance of natural food supply (Broom & Mason, 1978). The food supply in the spring and the rising temperatures increased gametogenesis of *Argopecten irradians* (Sastry, 1968, 1970a; 1975, Sastry & Blake, 1971; Blake & Sastry, 1979). Ansell (1974) observed that gonadal differentiation only began during the winter, with the main growth of gonad occurring after spring feeding of C. *septemradiata* in the Clyde Sea area. Ansell (1974) and Mackie (1986) suggested that the fecundity of many species may depend on reserves built-up in the previous spring and summer when phytoplankton levels are high. When food level is low, owing to bad weather conditions in summer, gonad development the following year depends entirely on the spring bloom. The effect of this situation is to cause low fecundity and poor recruitment (Duggan, 1987).

Although most of the work in this chapter was concerned with the dry weights of the main biochemical components, ash weights and water contents were also investigated. These also showed clear seasonal cycles. The adductor muscle ash weights of *A. opercularis* and *P. maximus* showed a seasonal variation over the two years similar to the variation in dry weights but of a lower magnitude. The highest ash contents were noted in autumn and the lowest values were in late winter or early spring. A similar pattern has been noted previously for various species of scallop (Comely, 1974; Mackie, 1986) and other bivalves (Daniel, 1920; Tanaka & Hatano, 1952; Giese, 1969), although no seasonal variations in adductor muscle ash was recorded by *A. opercularis* in the Clyde Sea (Taylor & Venn, 1979). Ash content of the gonads of both species also showed clear seasonal variations similar to those of gonad dry weights, while the 'other tissues' (mantle tissue and digestive gland) usually had the highest ash contents in both species. Giese (1969) attributed the high ash weights of the digestive glands

of *Tivela stultorum, Mytilus edulis* and *Modiolus demissus* to the higher content of lipids in this tissue.

The texture of adductor ash was notably different from gonad ash. Adductor ash was soft and white in colour for the two species, as noted also for *P. maximus* in the Clyde Sea (Comely, 1974). Gonad ash had a crystalline and granular form, especially when the gonad was in a more developed condition. This difference in the texture of ash presumably results from the different chemical compounds in the two tissues, as noted by various workers in other species (Tanaka & Hatano, 1952; Nair & Saraswathy, 1970; Comely, 1974; Tsuji & Nishida, 1988).

Generally the percentage of water showed an inverse relationship with the dry weight of particular body components of both species during the study. Thus, when the dry tissues increased in weight during the summer (adductor muscle, mantle tissue and digestive gland) or winter (gonad), the water content decreased. Although water content changed seasonally in the tissues, it remained relatively constant compared with the other biochemical components (Schmidt-Nielson, 1975).

Certain body components of the two species contained considerable water, for example, the mantle tissue and the gill (85% - 90%). The gonads showed some variability (between 76% - 86%), adductor muscle was intermediate (74% - 80%) while the digestive gland had the lowest water content (68% - 79%). These water levels are similar to previous observations (Comely,1974; Soemordihardjo, 1974; Taylor & Venn, 1979).

The increase in water level in the adductor muscle during the winter and spring results from extra fluid taken into the spaces left when the tissue is

broken down. As the muscle is subjected to loss of protein, coupled with increase in water, the water to protein ratio increases rapidly. The water/ protein ratio will therefore undergo similar variations to the weights of the tissues, but with a much greater magnitude, due to the interrelationship of protein and water (Schmidt-Neilson, 1975; Eckert & Randall, 1983). The water to protein ratio of the adductor muscle has therefore been used as a means of estimating the condition of the meat for commercial purposes (A.R. Brand, personal communication).

The variation in percentage water in the gonads of both species may be caused by a different process from that in the other tissues, as suggested by Soemodihardjo (1974) to account for the high fluctuation noted throughout the study period. The results for both *A. opercularis* and *P. maximus* indicated that absorbtion of free sea water by the newly-spent gonad increased its normal weight many times. Taylor & Venn (1979) observed higher fluctuation of gonad weights compared with the other tissues due to the water content of *A . opercularis* from the Clyde Sea area, and Comely (1974) noted similar results for *P. maximus* in the same area. Stanley (1967) and Soemodihardjo (1974) indicated that the high fluctuation of water level in the gonad should be treated separately from other tissues to get a clear picture. However, the balance of water in the tissues is under osmoregulatory control throughout the animal's life (Prosser & Brown, 1962; Schmidt-Nielson 1975; Eckert & Randall, 1983).

Although the seasonal cycles of the biochemical components discussed above were broadly similar, there were some notable differences in both the amplitude and the timing of the cycles between the two species, the populations of each on the two fishing grounds and the two years of study. For both queens and scallops, stored reserves of protein, lipid and

carbohydrate were higher in the Port St. Mary population and seasonal cycles were generally 1-3 months earlier in the year. In general, the first year of study (1991/92) resulted in higher energy reserves for queens and the second year (1992/93) for scallops. These differences in the cycles are closely related to the differing gametogenic cycles described in Chapter 1 and to environmental differences affecting the acquisition and expenditure of energy. The integration of these different physiological cycles and their synchronisation with environmental factors is discussed in the General Discussion.

4. GENERAL DISCUSSION

The occurrence of seasonal cycles of gametogenesis, coupled with cycles of energy storage and utilization, is not surprising for poikilothermic animals living in a strongly seasonal environment. In species like the pectinids, which undergo gametogenesis during the winter when food is less available, stored reserves must contribute to reproductive demands as well as to the energy maintenance demands of the body (Bayne, 1976; Sastry, 1979; Barber & Blake, 1981).

The seasonal cycles of two closely-located Irish Sea populations of *Aequipecten opercularis* and *Pecten maximus* have been described in detail in the preceding chapters. The extent to which the cycles described are synchronised and controlled by environmental factors, together with the occurrence of genetic determination, remain to be discussed.

Aequipecten opercularis and *Pecten maximus* have a similar geographical range and are frequently found on the same grounds (Mason, 1983; Brand, 1991). The spawning cycles of the two species have been found to be generally very similar, with gametogenesis closely tied to the seasonal changes in biochemical composition and weight of the adductor muscle and other tissues (Comely, 1974; Soemodihardjo, 1974; Taylor & Venn, 1979). The main difference between the two species appears to be that the early, winter/spring, partial spawning clearly observed in *A. opercularis*, is not generally present in *P. maximus* (Mason, 1958a; Duggan, 1987).

The results of the present study showed that gametogenesis in both populations occurred during the winter and reached a maximum in

early spring, after which ripe gametes were available for spawning. The timing of spawning in scallops is determined by a combination of internal and external factors (Sastry, 1976, 1979; Barber & Blake, 1991) which synchronise mainly with the presence of high food levels and maximum temperatures (Sastry, 1979). The synchronisation of spawning peaks with food supply and temperature has been observed for many species of bivalve (Sastry, 1961, 1963, 1979; Wakui & Obara, 1967; Sastry & Blake, 1971, Bayne & Worrall, 1980; Shafee & Lucas, 1980; Appeldoorn, 1983; MacDonald & Thompson, 1985a, b; Wolff, 1987, 1988). Variation in spawning synchrony from year to year has been studied by Langton *et al.* (1987) for mature *Placopecten magellanicus*.

In pectinids, after the release of gametes to the environment, fertilization occurs externally from random contact of male and female gametes. For this to occur, however, it depends upon the co-ordination of spawning between individuals to result in the synchronous release of male and female gametes, thereby increasing the chances of successful fertilization. This results in the production of large numbers of larvae (Sastry, 1979). Synchronous release of gametes between closely-located individuals is important for the hermaphroditic *A. opercularis* and *P. maximus* because they release eggs and sperm separately. This would help in the cross fertilization of different individuals in the population and may create the chance of fertilization with distant populations (Sastry,1979; Barber & Blake, 1991).

The degree of synchronization of spawning can vary seasonally within a population or between populations in different parts of the geographical range (Kinne, 1970; Sastry, 1979). A highly synchronised spawning, which would potentially allow the most effective fertilization, might be

an early indication of year class strength. Synchronicity is common in invertebrates living in high latitudes (Ockelmann, 1958). However, even in the tropics, breeding seasons appear to be limited to set periods, with spawning peaks suggesting some degree of synchronization (Gunter, 1957; Kinne, 1970).

The advantage of timing spawning to within a limited period during the summer is that the animal may take advantage of an abundance of food for the larvae (Sastry, 1966a, 1968; Bayne, 1975, 1976; Graf *et al.*, 1982; Christensen & Kanneworff, 1985), high water temperatures (Giese, 1959a; Vernberg, 1962; Kinne, 1962; Giese & Pearse, 1974; Bull, 1976) and long light periods (Sastry, 1970a), these being the best conditions for larval survival and growth (Thorson, 1950). Various environmental or other factors may act as triggers to stimulate spawning (Sastry, 1979).

There are some problems in investigating the degree of spawning synchronisation in scallop populations. Of the three methods used in the present study for determining the gametogenic cycle, all are potentially good for detecting the occurrence of closely-synchronised complete spawnings in a population (although the long sampling interval restricted their usefulness in this work) but are not very good for detecting poorly-synchronised partial spawnings or continuous 'trickle' spawning.

4.1 Synchronisation with productivity cycles

Phytoplankton abundance and reproductive activity are closely associated in some bivalve species (Kennedy & Krantz, 1982; Hummel, 1985; MacDonald & Thmpson, 1985a, b; Wolff, 1988, MacDonald &

Bourne, 1987; Couturier, 1993; Villalejo-Fuerte & Ochoa-Baez, 1993). Breese & Robinson (1981) stimulated a number of bivalves *(Crassostrea gigas* and C. *rivularia)* to spawn by holding them with high concentrations of phytoplankton. Sastry (1961, 1963, 1966a, 1970a) observed gonad growth and gametogenesis of *Argopecten irradians* in the presence of phytoplankton. Stanley (1967) and Lubet *et al.* (1987) noted the onset of gametogenesis and oocyte maturity in *Pecten maximus* to occur when high food levels were available. Broom & Mason (1978) observed three spawning in *Aequipecten opercularis* with an abundance of phytoplankton.

The availability and abundance of food for scallops depends largely upon productivity cycles in the Irish Sea (Allison, 1993). The hydrography of the Irish Sea is complex and has been the subject of a number of studies (Ramster & Hill, 1969; Brander & Dickson, 1984; Dickson & Boelens, 1988). The net flow of water throughout the year is generally considered to be northwards, around the Isle of Man. The surface currents are thought to follow this pattern, splitting at the south-west point of the island and flowing up the east and west coasts (Ramster & Hill, 1969) (Fig. 4.1). A recent study by Backhaus & Hainbucker (1987), however, emphasised the potential complexity of the current flow around the island and indicated that, during June, July and August, the water flow is in a predominantly southerly direction in the western Irish Sea. In addition, it was suggested that the current systems on either side of the island could be regarded as partially isolated. This may be true during the summer months when tidally-induced frontal systems separate regions of stratified and mixed water masses located around the Isle of Man (Pingree & Griffiths, 1978) (Fig. 4.2). The stratified waters contain the highest phytoplankton standing crop (Williamson, 1952, 1956) but

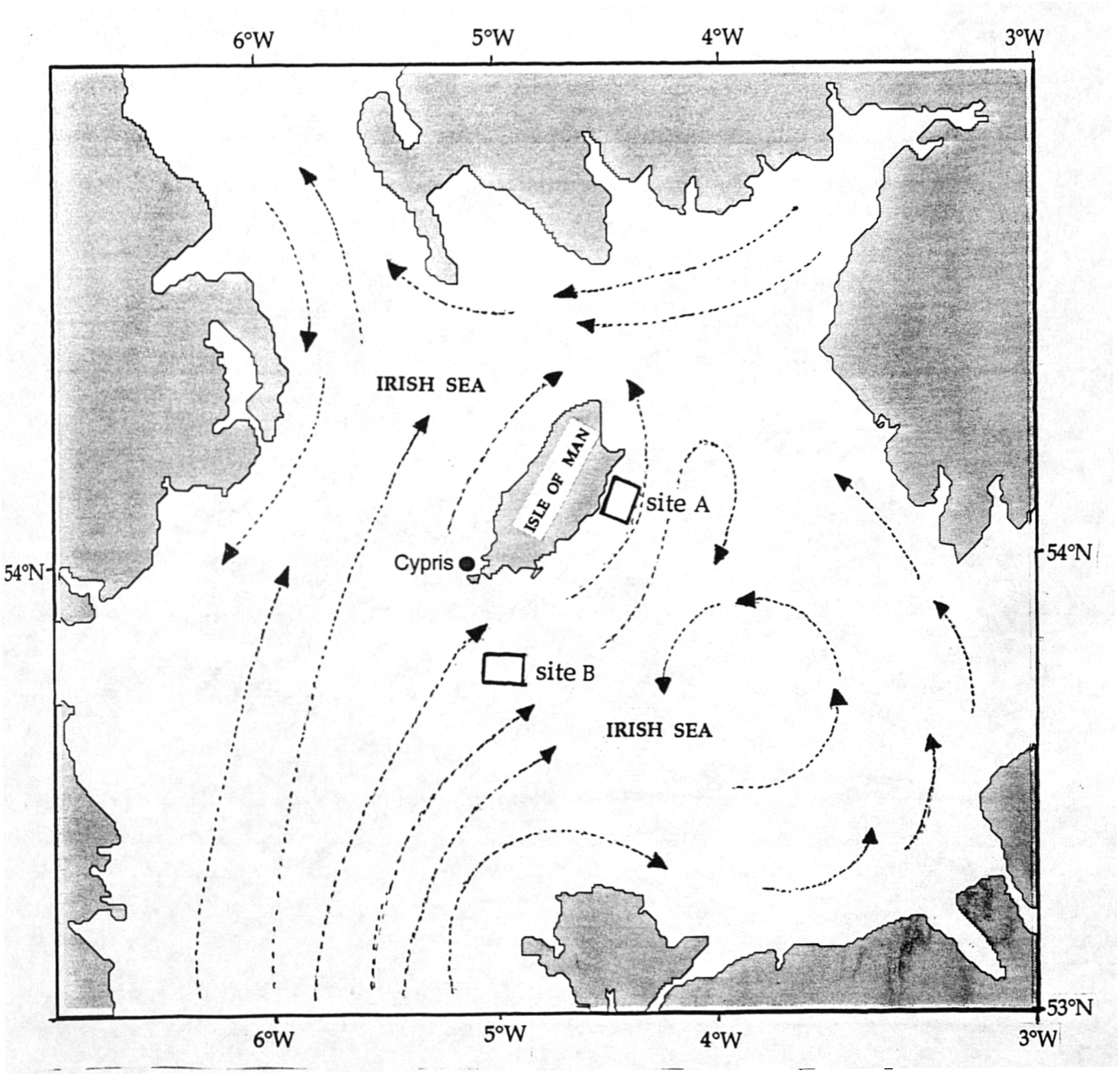


Fig. 4.1. Diagram showing main flow of surface currents in the Northern Irish Sea (redrawn and simplified from Ramster & Hill, 1969), together with position of 'Cypris' station (54° 05.5′ N 04° 50′ W) and sampling site A (Laxey Bay) and B (Port St. Mary).

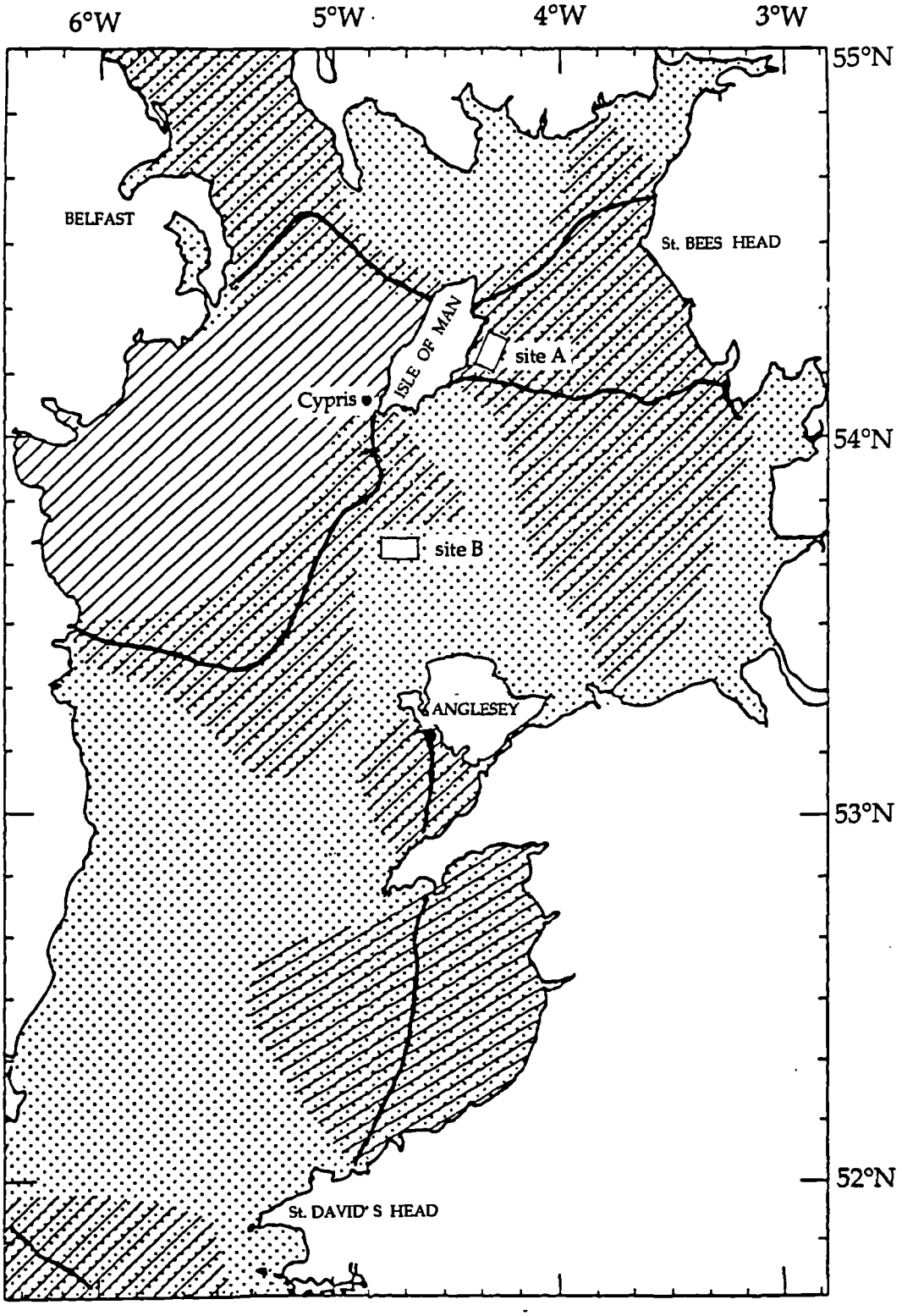


Fig. 4.2. Summer hydrographic conditions in the Irish Sea as predicted from the numerical model of Pingree & Griffiths (1978). Hatched areas indicate stratified waters; stippled, mixed areas; both, transitional waters.
(site A = Laxey Bay, site B = Port St. Mary)

the flux of energy to the benthos is higher and more rapid in the strongly mixed areas (Wafar et *al., 1983;* Graziano, 1988). The frontal areas themselves are rich in nutrients which results in high primary, secondary, microbial and benthic productivity (Reid, 1978; Grebmeier *et al.*, 1988; Allison, 1993; Lawrence, 1993).

The inshore Laxey Bay ground is in an area of transitional water near to the weak fronts which frequently form in the summer months to the east and north of the Isle of Man. The Port St. Mary ground is in mixed waters, to the east of the strong southwestern front, but the benthos in this area may benefit from the proximity of the front. It is also subjected to stronger tidal currents.

It was originally thought that the primary production cycle in the North Irish Sea was characterised by a bimodal spring and autumn bloom with the main peak in standing crop developing by May (Burrows & Sharples, 1973; Slinn, 1974). These observations were based on studies in the stratified water to the south and west of the Isle Man (Slinn, 1974) and from an area of haline stratification along the English coast at Liverpool Bay (Burrows & Sharples, 1973). More recent studies, however, have indicated that, for the extensive areas of mixed water, the phytoplankton bloom develops more typically in April/May to a single late peak in June or July (Colebrook, 1979; Brander & Dickson, 1984; Graziano, 1988; Fernandes, 1993).

Unfortunately, no data were collected on phytoplankton or chlorophyll *a* concentrations in the bottom water over the Laxey Bay and Port St. Mary fishing grounds, throughout the period of this study. The nearest relevant data for this time period is that for chlorophyll *a* concentrations

at the 'Cypris' station, 5 km off Port Erin (Fig. 4.3) (data courtesy of J.R. Allen). These data are of limited value as the 'Cypris' station is on the edge of the stratified area where it is subjected to very variable hydrographic conditions (Slinn & Eastham, 1984).

This may account for the very different pattern of chlorophyll *a* concentration recorded during the two years of this study, which shows evidence of spring and autumn peaks in 1991 and a single, late, summer peak in 1992. Reid (1978) and Graziano (1988) have observed that, generally, maximum chlorophyll *a* concentrations occur during the summer in both stratified and permanently well-mixed waters in the Irish Sea. It would, therefore, appear that the major spawning period during the summer, which occurred in the present study for both species, and on both grounds, is synchronised with the summer peak of phytoplankton production. Duggan (1987) observed similar synchronised summer spawnings of *A. opercularis* and *P. maximus* on two grounds (Bradda Head and Chickens) around the Isle of Man which corresponded with peak phytoplankton blooms.

Although, the major spawning peak of both scallops and queens occurred during the summer, the Laxey Bay populations spawned somewhat earlier than the Port St. Mary populations, particularly for *A. opercularis*. This also is in keeping with the different seasonal productivity cycles of the two areas described above. Likewise, the autumn spawning peak of both species, which occurred only in the Laxey Bay populations, coincided with the autumn peak of phytoplankton production which follows the breakdown of the thermocline in stratified or transitional waters (Graziano, 1988; Steingrimsson, 1989).

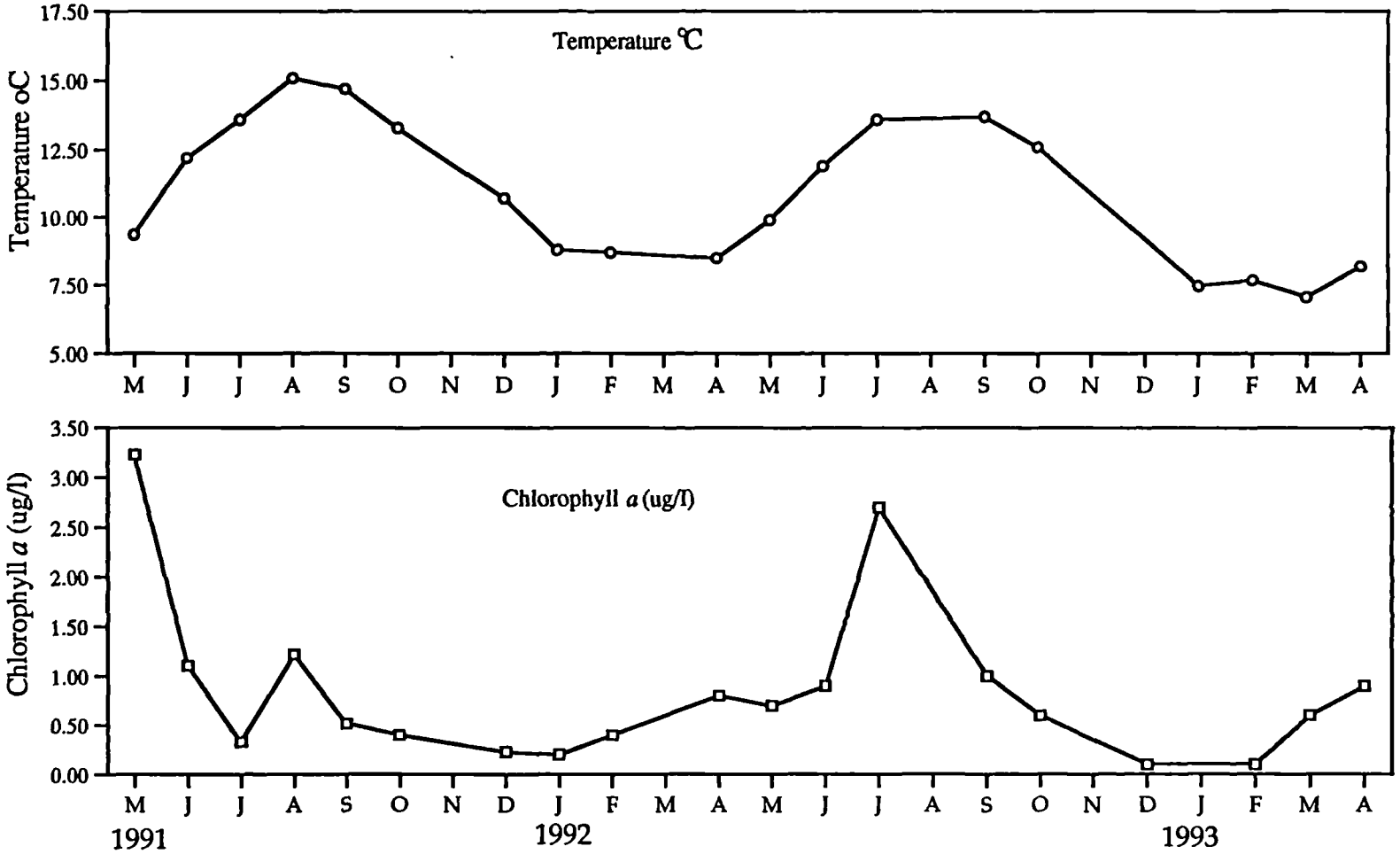


Fig. 4.3. Seasonal variation in mean surface column water temperature (°C) and chlorophyll *a* concentration (ug/I) from the north Irish Sea (Cypris station) during the study period. (data courtesy of J.R.Allen)

4.2 Synchronisation with temperature

Temperature has been considered to be another important synchronising factor for a number of bivalves, with spawning often occurring only at specific temperatures (Loosanoff, 1953; Sastry, 1963, 1966; Beukema *et al.*, 1985). Spawning of bivalves can be delayed or advanced by variations in temperature conditions from year to year (Loosanoff & David, 1951; Bayne, 1965; Naidu, 1970). Temperature gradients are common as stimulants for spawning of many bivalves as well as other aquatic animals (Sastry, 1979).

Wakui & Obara (1967) and Maru (1976) observed that *Patinopecten yessoensis* initiated gonad development when water temperature was low and the period of gonad growth coincided with increasing temperature. Similarly, Burnell (1983) noted that, in *Chlamys varia,* gametogenesis was initiated at a low temperature and gonad growth was correlated with rising temperature and high chlorophyll levels. Sastry (1970a) observed that primary germ cells developed in *Argopecten irradians* during winter and early spring, gamete differentiation began in late spring and the population reached maturity in summer in conjunction with an increase in temperature.

The results of the present study indicate that the seasonal spawning peaks may well be influenced by sea temperature but are not direct responses to particular temperatures. The maximum water temperature at the 'Cypris' station (Fig. 4.3) (data courtesy of J.R. Allen) in the summer 1991 was 14.1°C while the minimum recorded in winter was 8.1°C. Similarly, in 1992, the maximum and minimum were 13.6°C and

7.4°C respectively. This indicates that temperatures were slightly higher in 1991 than in 1992. Slinn & Eastham (1984) and Graziano (1988) observed that the annual surface-bottom temperature difference at the 'Cypris' station (37 m) was never more than 2°C during their studies. Slinn (1974) concluded that surface-bottom temperature differences in the north Irish Sea rarely exceeded 3.0°C, even where the water column reached its greatest depths (100m). Therefore the 'Cypris' station water temperatures are considered to reflect general temperature patterns for the north Irish Sea.

The main summer spawnings of both *A. opercularis* and *P. maximus* occurred during the period when temperature was rising rapidly but spawning was clearly not triggered by any particular temperature. Recovery of the gonads after spawning occurred when both water temperature and phytoplankton availability was falling.

Amirthalingam (1928) stated that, as long as the temperature remained below 11°C, spawning of *A. opercularis* at Plymouth occurred normally but when the temperature rose above 11°C spawning did not occur. Soemodihardjo (1974) and Duggan (1987) found no indication of an upper limit of 11°C for *A. opercularis* and *P. maximus* in Manx waters. Mason (1958a), studying *P. maximus* around the Isle of Man, observed no direct correlation but noted that temperature probably affected gametogenesis. Strand & Nyland (1991) noted that the *P. maximus* population at Fosen, northern Norway, spawned in June at a temperature of 7-8°C in 1987 and 8-9°C in 1988, while a more southerly population at Austevoll spawned in August- September at a temperature of 13-15°C. They concluded that spawning in these two populations was triggered by different external controls. Similarly, field observation by

Aravindakshan (1955) and Soemodihardjo (1974) seem to rule out any simple effects of both temperature and food, as the time of spawning of *A. opercularis* showed little correlation with either factor.

4.3 Other exogenous and endogenous factors synchronising spawning

Some other exogenous factors may also act as stimuli for the spawning process and could serve to synchronise spawning of a population. Factors potentially triggering spawning, include photoperiod (Segal, 1970; Giese & Pearse, 1974; Sastry, 1979) and lunar periodicity (Orton, 1926; Grave, 1927; Battle, 1932; Amirthalingam, 1928; Tang, 1941; Yamamoto, 1952; Mason, 1958b; Stanley, 1967), but dissolved oxygen, pH, mechanical shock and various chemicals have also been examined in both the laboratory and the field and could be involved (Barber & Blake, 1991). In *Chlamys varia* (Lubet, 1951; 1955), spawning was stimulated by the presence of gametes of the opposite sex and this appears to occur in other species (Sastry, 1979). Thus Coe (1945) observed that water containing sperm and eggs stimulated spawning in populations of *Pecten circularis* and other pelecypod molluscs. Wada (1954) reported that the addition of an egg/ water suspension or a sperm suspension stimulates spawning in tridacnid clams. This type of stimulus could contribute towards the synchronisation of spawning within an area.

The effects of endogenous regulation on the spawning cycle of pelecypods have been studied on many occasions (Martoja, 1972; Golding, 1974; Sastry, 1979). Endogenous regulations are mainly controlled by nervous and hormonal systems which are interrelated structurally and funtionally (Sastry, 1979). The nervous system is involved in neurotransmission as well as in the synthesis and discharge

of secretions (Blaschko & Milton, 1960; Blake & Sastry, 1979; Barber & Blake, 1991). Neurons secrete both neurohumors and neurohormones (Sastry, 1979; Matsutani & Nomura, 1982). The relationship between neurosecretory products and scallop spawning has been studied recently (Barber & Blake, 1991). Matsutani & Nomura (1982) and Tanaka & Murakoshi (1985) observed that the neurosecretory product serotonin (5-hydroxytryptamine) effectively induced spawning of *Patinopecten yessoensis* and *Pecten albicans*. Matsutani & Nomura (1986) found that serotonin inhibits a hormone in the nervous system which prevents spawning.

It is clear that gametogenesis and the spawning cycle of pectinids is regulated by a combination of external (mainly food and temperature) and internal (neurosecretion) factors which synchronise the cycle for the production and survival of the maximum number of gametes in order to maximise recruitment to the adult population. The greater food availability and higher temperatures during the summer enhance shell formation and improve the chances of avoiding winter mortality.

4.4 Depth

Depth is often implicated as a factor influencing many aspects of the biology of pectinids, including growth rate in terms of shell length (Mason, 1957; Baird, 1966; MacDonald, 1985a; Thouzeau *et al.*, 1991; Allison, 1993), weight of somatic tissues (MacDonald & Thompson, 1985a, 1985b), and allometric relationships between length and weight (Hayne, 1966; Schick & Shumway, 1986; Worms & Davidson, 1986).

Variation in gametogenesis has been noted between sites of differing water depth in several different studies. The deeper water environments may be considered to be generally less favourable for scallop growth and gametogenesis because they are colder and have less food available to suspension feeding bivalves. MacDonald & Thompson (1985) observed a slower growth rate of the shell, and somatic tissues were in poorer condition for *Placopecten magellanicus* in deep waters; Caddy *et al.*, (1970) and Posgay (1979) came to the same conclusions. Mason (1957) and Murphy (1986) showed a similar trend of decreasing shell growth with increasing water depth for *Pecten maximus* in the North Irish Sea. All these differences were related to food and temperature conditions within the habitats. Thus Allison (1993) indicated that tidal currents, differences in depth, temperature and food availability may all effect the growth of *A. opercularis* and *P. maximus* in Manx waters and many of these factors are often interrelated.

The results of the present study also suggest that depth may have influenced certain aspects of gametogenesis and spawning on the two grounds. Both *A. opercularis* and *P. maximus* populations in Laxey Bay (20 - 30m depth) showed a distinct autumn spawning but this was absent for both species from the Port St. Mary ground (50 - 70m depth). The reason for this marked difference in the spawning cycle between two relatively closed-located areas is not clear. The bottom water temperatures may be slightly lower at the deeper offshore ground, but this is unlikely to be very important in such a strongly tidally-mixed area (Slinn, 1974). The different spawning cycles are more likely to be related to differences in food availability resulting from the different hydrographic conditions at the two grounds. Lawrence (1993) suggested that food quantity is not a limiting factor for *A. opercularis* or *P.*

maximus in the tidally-mixed areas of the north Irish Sea but considered that food quality was important. No information is available on the quantity or quality of food available to scallops and queens on these two grounds, though it seems likely that the flux of energy to the benthic boundary layer where these pectinids feed would be greater on the Port St. Mary ground through the summer months. Benthic diatoms however would probably be more abundant in the shallower Laxey Bay.

MacDonald & Thompson (1986), comparing populations of *Placopecten magellanicus* at depths of 10m and 31m, showed a reduced rate of gamete development at the deeper site, although the size of spawned eggs was similar at both sites. Barber *et al.* (1988) compared gametogenic cycles of the same species at much greater depth variation (13 - 20m and 170 - 180m) and observed that the gonad weight and gonadal index for individuals of similar shell height was significantly greater for animals from the shallow depth. They concluded that it is the factors that vary with depth, mainly food and temperature, which affect gametogenesis.

In contrast, Richardson *et al.* (1982) reported that water depths ranging from 20-40m had no influence on shell growth of cultured *A. opercularis* from the Firth of Clyde and Gruffydd (1974) came to the same conclusion when studying natural populations of *P. maximus* in the North Irish Sea.

4.5 Other factors affecting feeding

In addition to temperature and water depth, various other environmental factors can affect the seasonal build-up of energy reserves, mostly through their effect on feeding. These include current

flow rates, substrate type, silt, fishing and fouling, all of which can produce localised variations in gonad and somatic growth (Baird, 1958; Mason, 1983; MacDonald & Thompson, 1985a, 1985b; Barber & Blake, 1991; Allison, 1993).

Low somatic weights in certain areas may be influenced by mud substrates which are indicative of reduced water flow (this reduces the availability of suspended food). The influence of fine silt on respiration and feeding efficiency may reduce growth (Vahl, 1980; Wallace & Reinsnes, 1985). Vahl (1980) observed slow growth of *Chlamys islandica* in areas where mud is present due to reduce water flow. Gruffydd (1974), Murphy (1986) and Allison (1993) observed reduced growth of *P. maximus* in the Irish Sea associated with high silt contents of the substrates. Although no detailed analyses were made of the substrates in the two sampling areas the Laxey Bay ground undoubtedly contained a higher proportion of silt than the Port St. Mary ground.

The effects of fishing activity on growth are not clear. Dredging and trawling oprerations re-suspend benthic detritus, possibly increasing available food but they also re-suspended quantities of silt which probably reduce feeding efficiency (Allison, 1993). Heavy fishing may therefore reduce the time the scallop spends in filter feeding causing a reduction of energy intake and resulting in lower growth. This would probably be of rather greater magnitude on the inshore Laxey Bay ground where fishing effort in considerably higher than further offshore (Brand *et al.*, 1991).

Size-selective fishing may also affect long-term somatic growth pattern (Allison, 1993). The main environmental changes believed to have

occurred on the scallop fishing grounds in recent years are a decrease in scallop density (Brand *et al.*, 1991b) and possible ecological changes in benthic community structure as a result of dredging (MacDonald, 1993; Allison, 1993). Heavy dredging increases mortality and causes direct damage to many animals. Size selective fishing could generate the selection pressure required to alter the pattern of growth of scallops (Allison, 1993). Fishing pressure has already been implicated in causing the reduction in size at first sexual maturity and growth rate in cod (Law & Grey, 1989; Jørgensen, 1990). Smith *et al.* (1991) observed the loss of genetic diversity in the New Zealand stock of orange roughy, resulting from fishing.

On the scallop fishing grounds around the Isle of Man heavy fishing on the inshore ground has resulted in populations dominated by the recruiting year class (Brand *et al* ., 1991a). Younger animals have a lower fecundity (Thompson & MacDonald, 1991) so that, together with the decrease in scallop density, the reproductive output of the stocks on the inshore fishing grounds, like Laxey Bay must have fallen enormously in recent years. One further concern arising from the very low densities on the inshore grounds is the possible effect that this could have on the success of fertilization. This problem has been discussed for the giant scallop *Placopecten magellanicus* (Stokesbury & Himmelman, 1993)

The final environmental factor which may influence growth and the build-up of metabolic reserves is the presence of fouling organisms on the shell. In the present study of *A. opercularis* from Laxey Bay, 100% of the animals age 1-4 years were at least to some extent covered by epifaunal species of sponges, barnacles, anomiids and hydroids, all of which were much more common on the upper valve (Sole-Cava &

Thorpe, 1986; Ward & Thorpe, 1991). On the other hand the shells of the Port St. Mary population of queens were fouled to a lesser degree. The fouling organisms (except sponges) on *P. maximus* showed a similar pattern over the two grounds. Increased fouling may reduce swimming activity (especially for queen scallop) and reduce shell opening (Chapman *et al.*, 1979). Since most fouling organisms are also filter feeders they compete with the pectinid for food and any resulting limitation on food intake may cause low somatic growth (Kay & Keough, 1981; Keough, 1984).

With so many interacting factors affecting feeding, it is not possible to account for the earlier and greater build-up of metabolic reserves in the Laxey Bay compared with Port St. Mary populations of queens and scallops, or to attribute the difference to particular environmental factors. This would require a detailed study of the ecological energetics of these two populations and more precise field data on the environmental conditions at the two grounds.

4.6 Geographical variation in oocyte lysis

While the metabolic reserves built up in the adductor muscle, digestive gland and other tissues during the spring and summer appeared to be sufficient to allow gametogenesis to proceed in the autumn and winter for both populations of *A. opercularis* and *P. maximus* investigated in this thesis, this is not always the case in other populations. For some scallop populations it would appear that the gonads themselves provide the source of energy to increase the weight of the adductor muscle in autumn (Lubet *et al.*, (1987a, 1987b; Faveris & Lubet, 1991). In *P. maximus* from the Bay of Seine (English Channel) only spawnings from

July - August are important for recruitment but mature animals are found from November to the following September. Cytological examination of the gonads of these populations has shown the occurrence of oocyte lysis, several generations of oocytes being destroyed and the products of this lysis being reabsorbed as an energy reserve (Lubet *et al.*, 1987a; Besnard 1888). Faveris & Lubet (1991) conclude that oocyte lysis plays a role in supplying the necessary metabolites to maintain the physiological integrity of the animal during the difficult part of the year (winter and early spring).

Lubet *et al.* (1987a, 1987b) and Ansell *et al.* (1991) suggest that the occurrence of oocyte lysis differs over the geographical range owing to variations in genetic and environronmental conditions. Populations in different parts of the English Channel show well-marked differences. For example, highly synchronous maturation of individuals of the native scallop, *Pecten maximus*, in the Bay of St. Brieuc on the northern coast of Brittany showed lysis of oocytes from April to July (Bergeron & Buestel, 1979; Ansell *et al.*, 1988; Paulet *et al.*, 1988; Dorange & Pennec, 1989). In contrast, in the relatively closely-located Bay of Brest, the population shows little synchrony, and lysis of oocytes occurs from December to July (Cochard, 1985). Ansell *et al* (1991) suggested that the occurrence of high numbers of atretic oocytes at certain times of the year seems to be characteristic of populations from shallow, warmer water in the more southerly part of the region similar to Bay of Seine (Lubet *et al.*, 1987; Paulet *et al.*, 1988) but oocyte lysis has been recorded in some of the most northerly *P. maximus* populations (Strand & Nyland, 1991). Similar physiological strategies in relation to metabolic reserves have been described in various other bivalves and gastropods (Joose *et al.*, 1968;

Jong-Brink, 1969, Jong-Brink, 1973; Griffond; 1977a; Jong-Brink *et al.*, 1983; Pipe, 1987).

This raises the possibility that the autumn spawning of Irish Sea scallops is not totally a spawning event, but a mass lysis of oocytes which formed over the late summer. This spawning or lysis coincides with a period of increase in adductor muscle weight in autumn and may have evolved as a strategy for storing excess energy by transfer to the adductor muscle, which acts as the main energy storage site over the winter. Some support for the occurrence of autumn lysis comes from the observation that the major spawning period was in the summer, rather than the autumn, for both species. Allison (1993) also observed that the autumn spawning of Irish Sea scallops occurred after the main spatfall had already taken place, and Brand *et al.* (1991a) suggested that it may represent oocyte lysis rather than a spawning event. This remains speculative, however, since no histological or cytological studies have been performed to demonstrate lysis for Irish Sea scallop populations.

4.7 Genetic regulations of seasonal cycles

Although the seasonal cycles of scallops are undoubtedly synchronised and controlled by various environmental factors, there is increasing evidence that genetic factors play a significant role in controlling the gametogenic cycle (Ansell *et al.*, 1991). In recent years many studies have been carried out on *Aequipecten opercularis* and *Pecten maximus* to determine their genetic variability (Beaumont, 1982a, 1982b, Beaumont & Beveridge, 1984; Macleod *et al.*, 1985; Duggan, 1987; Beaumont & Zouros, 1991; Lewis, 1992). Some studies have shown that closely located scallop stocks can vary in their gametogenic cycles indicating intra-

specific differences (Lubet *et al.*, 1987; Paulet *et al.*, 1988). Certain populations of *P. maximus* in the English Channel are examples of this (Lubet *et al.*, 1987; Ansell, 1991). Evidence for the genetic basis of gametogenic cycles comes also from transplant experiments.

A group of young scallops were taken from spat collectors from the west coast of Scotland and from hatchery reared stock taken originally from a population in the Bay of Brest. These two populations were then transplanted into the Bay of St. Brieuc (Halary *et al.*, 1982; Dao, Buestel & Halary, 1985; Dao *et al.*, 1985; Boucher, 1985). Comparision of spawning cycles of native St. Brieuc scallops with those of Scottish and Bay of Brest transplants showed that, in both groups of transplants, recovery of the gonad began in late summer and the mean state of maturity then diverged progressively from that of the St. Brieuc natives, in which recovering is delayed until the following spring. The spawning event also remained less well-synchronised between individuals in the transplant scallops than in the St. Brieuc natives. These results showed that genetic factors play a significant role in controlling the features of the reproductive cycle in these stocks (Ansell *et al.*, 1988, 1991). These results are further strengthened by hatchery conditioning experiments with *P. maximus* from the same native and transplant populations (Devauchelle & Cochard, 1989). The fact that Scottish *P. maximus* adapted easily to transplantation to French waters was attributed by Huelvan (1985) to their high genetic variability; transplantations were less successful in the more genetically homogeneous scallops from Irish locations.

Genetic studies of *Aequipecten opercularis* (Mathers, 1975; Beaumont, 1982a, b; MacLeod *et al.*,1985; Lewis, 1992) provide evidence that there is a

considerable degree of genetic separation between stocks in different parts of the geographical range of this species. Beaumont (1982a, b) concluded that there are at least four genetically-isolated populations of *A. opercularis* around the British Isles. Beaumont's results also indicated that for *A. opercularis* there is probably little exchange of pectinid larvae between populations in the Bay of St. Brieuc and populations further to the west (Bay of Brest) causing at least partial genetic isolation; this would account for the reproductive differences of scallop populations in this area. A recent study of *A. opercularis* populations around the Isle of Man, based on very large sample sizes (Lewis, 1992), concluded that there was strong evidence of at least partial genetic isolation between various populations.

Studies of the reproductive ecology of different populations of pectinids that are genetically isolated stocks, or in different growth areas, have important implications for stock assessment, for restocking and other management programmes. Such knowledge is also important for aquaculture operations which may involve transfers of stock from one area to another.

4.8 Future work.

The work described in this thesis has shown how the seasonal cycles of spawning, energy storage and energy utilization can differ in populations of *A. opercularis* and *P. maximus*, even in closely-located areas, and has discussed same of the complex mechanisms by which these cycle are integrated and controlled. Further work is now required to determine more precisely how hydrographic factors such as the proximity of tidal fronts and water depth interact with other environmental conditions to

affect the quantity and the quality of food available to these species. Scallops and queens have rather different morphological and behavioural adaptations (Brand, 1991) which could result in differences in the seasonal availability of food for populations in the same area; this could account for some of the differences in the seasonal cycles described in this thesis. In addition, since seasonal spawning cycles appear to be genetically determined, more detailed knowledge is required of the scale at which local populations are differentiated. Such knowledge could come from studies of polymorphisms using mitochondrial DNA as genetic markers.

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Appendix 3.1. Seasonal variations in the percentage composition of adductor muscle of *Aequipecten opercularis* (65 - 70 mm shell length) from the Laxey Bay and Port St. Mary. Values are % dry weight except for water (% wet weight). (Values represent means for 10 - 15 individuals) * not available

		Adductor muscle (Laxey Bay)					Adductor muscle (Port St. Mary)				
Year	Month	Protein	Lipid	Glycogen	Ash	Water	Protein	Lipid	Glycogen	Ash	Water
1991	May	78.31	3.57	1.01	10.81	77.10	73.28	3.66	5.44	8.54	78.44
	Jun	70.96	3.33	5.93	11.60	77.23	76.56	3.75	3.95	8.41	77.62
	Jul	66.66	3.29	10.66	11.72	76.90	72.04	3.85	7.73	10.70	77.60
	Aug	70.44	3.92	8.83	12.03	76.43	68.36	2.96	8.55	10.65	75.64
	Sep	72.14	3.73	10.58	11.65	76.14	68.31	3.41	8.99	9.33	75.85
	Oct	71.01	2.95	11.69	10.88	75.86	63.96	2.95	15.94	8.39	74.86
	Nov	70.60	3.50	10.17	11.09	76.88	65.87	3.52	11.82	10.10	73.55
	Dec	69.45	3.16	6.47	11.32	76.31	62.65	3.28	13.17	10.46	74.43
1992	Jan	72.95	3.50	5.40	12.64	77.50	63.77	2.95	14.33	11.25	75.76
	Feb	77.82	3.20	2.86	11.93	79.19	67.27	2.54	11.65	11.01	76.89
	Mar	76.29	3.19	0.73	10.78	78.94	75.71	3.37	4.59	11.09	78.44
	Apr	79.02	3.51	1.11	9.96	79.92	75.67	3.61	5.17	13.05	78.66
	May	79.30	3.58	1.15	11.66	76.20	73.89	3.59	5.46	13.29	78.14
	Jun	74.92	3.41	6.36	11.74	77.22	74.79	3.66	6.92	13.07	78.49
	Jul	66.96	3.31	11.84	9.94	75.71	66.01	3.53	10.21	12.03	75.31
	Aug	65.95	3.41	10.74	10.73	75.90	67.33	3.35	11.06	11.30	75.14
	Sep	*	*	*	*	*	65.38	3.10	9.51	10.13	75.05
	Oct	64.19	3.40	13.88	9.71	75.25	63.85	2.93	11.39	10.52	74.96
	Nov	65.95	3.06	13.97	9.45	75.05	65.79	3.05	13.06	12.13	76.40
	Dec	66.17	3.08	13.90	9.49	76.48	63.92	3.56	14.46	8.31	76.34
1993	Jan	77.90	3.69	8.32	7.87	78.52	71.34	3.90	8.32	9.21	78.53
	Feb	79.13	3.59	4.22	8.06	78.37	73.08	2.89	8.40	7.43	78.37
	Mar	81.53	3.79	2.13	8.33	79.15	74.31	2.94	8.16	8.59	79.63
	Apr	80.26	3.86	1.88	8.28	76.08	73.21	3.42	3.48	11.30	79.01

Appendix 3.2. Seasonal variations in the absolute content (in grams) of adductor muscle of *Aequipecten opercularis* (65 - 70 mm shell length) from the Laxey Bay and Port St. Mary. (Values represent means for 10 - 15 individuals)
* not available

		Adductor muscle (Laxey Bay)					Adductor muscle (Port St. Mary)				
Year	Month	Dry wt	Protein	Lipid	Glycogen	Ash	Dry wt.	Protein	Lipid	Glycogen	Ash
1991	May	1.313	1.028	0.047	0.013	0.142	1.412	1.034	0.052	0.077	0.121
	Jun	1.351	0.959	0.045	0.080	0.157	1.480	1.133	0.056	0.058	0.125
	Jul	1.519	1.013	0.050	0.162	0.178	1.479	1.066	0.057	0.114	0.154
	Aug	1.515	1.067	0.059	0.134	0.182	1.870	1.279	0.055	0.160	0.199
	Sep	1.655	1.194	0.062	0.175	0.193	2.176	1.486	0.074	0.196	0.203
	Oct	1.795	1.275	0.053	0.210	0.195	2.482	1.587	0.073	0.396	0.208
	Nov	1.747	1.233	0.061	0.178	0.194	2.504	1.649	0.088	0.296	0.253
	Dec	1.699	1.180	0.054	0.110	0.192	2.312	1.448	0.076	0.304	0.242
1992	Jan	1.560	1.138	0.055	0.084	0.197	1.935	1.234	0.057	0.277	0.218
	Feb	1.237	0.963	0.040	0.035	0.148	1.638	1.102	0.042	0.191	0.180
	Mar	1.152	0.879	0.037	0.008	0.124	1.459	1.105	0.049	0.067	0.162
	Apr	1.073	0.848	0.038	0.012	0.107	1.357	1.027	0.050	0.070	0.177
	May	1.323	1.049	0.047	0.015	0.154	1.436	1.061	0.052	0.078	0.191
	Jun	1.400	1.049	0.048	0.089	0.164	1.443	1.080	0.053	0.099	0.189
	Jul	1.566	1.048	0.052	0.185	0.156	1.829	1.208	0.065	0.187	0.220
	Aug	1.519	1.002	0.052	0.163	0.163	1.910	1.286	0.064	0.211	0.216
	Sep	*	*	*	*	*	1.931	1.262	0.060	0.184	0.196
	Oct	1.826	1.172	0.062	0.254	0.177	1.952	1.246	0.057	0.222	0.205
	Nov	1.893	1.248	0.058	0.265	0.179	1.685	1.108	0.051	0.220	0.204
	Dec	1.738	1.150	0.054	0.242	0.165	1.794	1.147	0.064	0.259	0.149
1993	Jan	1.501	1.169	0.055	0.125	0.118	1.441	1.028	0.056	0.120	0.133
	Feb	1.308	1.035	0.047	0.055	0.105	1.267	0.926	0.037	0.106	0.094
	Mar	1.229	1.002	0.046	0.026	0.102	1.079	0.802	0.032	0.088	0.093
	Apr	1.291	1.036	0.050	0.024	0.107	1.272	0.932	0.044	0.044	0.144

Appendix 3.3. Seasonal variations in the percentage composition of biochemical components in the testis of *Aequipecten opercularis* (65 - 70 mm shell length) from the Laxey Bay and Port St. Mary. Values are % dry weight. (Values represent means for 10 - 15 individuals) * not available

		Testis (Laxey Bay)			Testis (Port St. Mary)		
Year	Month	Protein	Lipid	Glycogen	Protein	Lipid	Glycogen
1991	May	67.70	6.31	6.13	74.16	5.99	4.55
	Jun	65.76	6.45	5.02	59.67	3.61	2.79
	Jul	68.20	5.63	3.32	72.80	5.30	5.55
	Aug	70.00	3.26	2.99	59.45	3.75	3.05
	Sep	57.54	4.87	2.45	62.67	5.70	3.57
	Oct	52.72	3.88	2.41	65.01	4.33	3.90
	Nov	52.23	4.36	3.82	57.85	3.42	2.43
	Dec	60.02	3.91	3.82	61.43	5.89	5.56
1992	Jan	64.59	4.34	4.73	66.99	5.14	6.29
	Feb	67.27	4.26	6.53	70.11	5.83	6.33
	Mar	67.72	5.00	5.34	65.69	4.90	5.16
	Apr	68.25	6.37	5.49	74.17	5.70	4.17
	May	67.81	6.30	5.24	73.10	6.23	5.00
	Jun	67.48	6.41	5.18	59.75	3.75	2.93
	Jul	68.37	5.79	3.39	64.09	7.96	4.11
	Aug	68.09	5.61	3.28	63.68	8.10	3.60
	Sep	*	*	*	59.90	7.71	3.86
	Oct	57.49	4.84	3.59	53.59	6.40	4.21
	Nov	58.19	6.30	3.62	59.72	5.18	6.53
	Dec	57.70	6.29	4.69	66.32	7.44	8.08
1993	Jan	65.63	6.66	4.75	65.87	6.79	7.55
	Feb	67.27	5.97	5.36	65.22	5.51	6.22
	Mar	68.03	7.31	7.08	63.86	5.61	5.69
	Apr	68.11	7.15	7.02	73.35	6.06	5.03

Appendix 3.4. Seasonal variations in the percentage composition of biochemical components in the ovary of *Aequipecten opercularis* (65 - 70 mm shell length) from the Laxey Bay and Port St. Mary. Values are % dry weight. (Values represent means for 10 - 15 individuals) * not available

		Ovary (Laxey Bay)			Ovary (Port. St. Mary)		
Year	Month	Protein	Lipid	Glycogen	Protein	Lipid	Glycogen
1991	May	55.02	21.60	3.66	57.64	18.74	5.12
	Jun	55.17	18.05	4.69	49.95	7.83	2.83
	Jul	59.06	17.71	3.23	57.97	9.55	5.33
	Aug	59.06	11.98	4.03	53.32	6.97	1.93
	Sep	54.36	5.98	2.54	53.43	14.14	3.12
	Oct	47.41	5.15	1.92	52.85	9.94	3.05
	Nov	46.61	9.42	2.57	48.13	6.60	2.32
	Dec	53.46	9.98	3.01	50.80	14.74	5.24
1992	Jan	50.91	10.52	2.89	51.68	15.62	5.79
	Feb	53.65	15.47	4.69	53.81	18.40	5.16
	Mar	54.23	18.49	4.36	54.26	19.37	5.22
	Apr	54.41	22.09	3.97	56.67	18.62	5.10
	May	54.36	20.93	4.15	56.75	19.28	5.04
	Jun	56.11	18.91	4.61	50.04	14.74	2.65
	Jul	59.65	17.84	3.24	56.00	17.59	2.94
	Aug	58.84	17.43	3.33	55.66	18.43	2.92
	Sep	*	*	*	52.82	13.70	3.35
	Oct	55.11	10.47	2.95	49.90	8.83	3.93
	Nov	52.06	11.21	4.68	50.31	11.42	6.16
	Dec	51.95	11.35	4.67	54.89	18.39	7.07
1993	Jan	53.90	15.98	3.78	53.05	19.93	6.81
	Feb	52.01	14.94	4.77	55.71	15.52	5.32
	Mar	55.67	23.96	7.16	56.02	15.58	5.46
	Apr	55.36	24.38	7.28	57.90	19.49	5.68

Appendix 3.5. Seasonal variations in the percentage composition of total gonad (testis and ovary combined) of *Aequipecten opercularis* (65 - 70 mm shell length) from the Laxey Bay and Port St. Mary. Values are % dry weight except for water (% wet weight). (Values represent means for 10 - 15 individuals) * not available

		Total gonad (Laxey Bay)					Total gonad (Port St. Mary)				
Year	Month	Protein	Lipid	Glycogen	Ash	Water	Protein	Lipid	Glycogen	Ash	Water
1991	May	61.36	13.96	4.90	13.31	76.85	65.90	12.39	4.84	12.14	82.87
	Jun	60.47	12.25	4.86	11.43	78.52	54.81	5.72	2.81	18.97	82.54
	Jul	63.63	11.67	3.28	12.07	80.04	65.38	7.43	5.44	15.15	80.33
	Aug	64.53	7.62	3.51	10.36	76.25	56.38	5.36	2.49	17.57	85.89
	Sep	55.95	5.43	2.50	12.04	81.92	58.05	9.92	3.35	17.36	84.16
	Oct	50.07	4.52	2.17	15.50	87.71	58.93	7.14	3.48	15.96	84.17
	Nov	49.42	6.89	3.20	19.59	87.45	52.99	5.01	2.38	15.92	82.25
	Dec	56.73	6.95	3.42	16.81	84.63	56.11	10.32	5.40	16.59	78.42
1992	Jan	57.75	7.43	3.81	13.47	81.14	59.33	10.38	6.04	17.41	77.92
	Feb	60.46	9.86	5.61	11.27	77.22	61.96	12.12	5.75	16.84	77.91
	Mar	60.99	11.75	4.85	13.08	79.47	59.97	12.14	5.19	15.12	77.95
	Apr	61.33	14.23	4.73	10.06	78.67	65.42	12.16	4.64	12.69	82.88
	May	61.08	13.62	4.70	13.00	76.59	64.92	12.76	5.10	13.20	83.96
	Jun	61.79	12.66	4.90	11.63	80.03	54.89	5.75	2.80	15.81	86.09
	Jul	64.01	11.82	3.32	11.57	79.04	60.05	12.76	3.50	12.03	77.49
	Aug	63.47	11.52	3.31	12.51	78.31	59.67	13.27	3.26	10.61	75.63
	Sep	*	*	*	*	*	56.36	10.71	3.61	11.76	81.08
	Oct	56.30	7.66	3.27	13.97	83.56	51.75	7.62	4.07	13.79	86.56
	Nov	55.12	8.76	4.15	22.17	89.47	55.02	8.30	6.30	13.06	83.91
	Dec	54.83	8.82	4.68	14.14	84.49	60.61	12.92	7.58	10.88	80.02
1993	Jan	59.76	11.32	4.27	10.68	80.80	59.46	13.36	7.18	10.39	77.98
	Feb	59.64	10.46	5.07	10.76	79.94	60.47	10.52	5.77	11.66	78.47
	Mar	61.85	15.64	7.12	10.35	79.58	59.94	10.60	5.58	11.79	78.95
	Apr	61.74	15.77	7.15	9.78	77.33	65.63	12.76	5.36	11.98	82.26

Appendix 3.6. Seasonal variations in the absolute content (in grams) of biochemical components in the total gonad (testis and ovary) of *Aequipecten opercularis* (65 - 70 mm shell length) from the Laxey Bay and Port St. Mary. (Values represent means for 10 - 15 individuals) * not available

		Total gonad (Laxey Bay)					Total gonad (Port St. Mary)				
Year	Month	Dry wt	Protein	Lipid	Glycogen	Ash	Dry wt	Protein	Lipid	Glycogen	Ash
1991	May	0.452	0.278	0.063	0.022	0.060	0.320	0.211	0.039	0.015	0.039
	Jun	0.393	0.238	0.048	0.019	0.045	0.231	0.127	0.013	0.006	0.044
	Jul	0.253	0.161	0.030	0.008	0.031	0.294	0.192	0.022	0.016	0.045
	Aug	0.569	0.367	0.043	0.019	0.059	0.166	0.093	0.009	0.004	0.029
	Sep	0.335	0.187	0.018	0.008	0.040	0.168	0.098	0.017	0.006	0.029
	Oct	0.077	0.039	0.003	0.002	0.012	0.162	0.095	0.012	0.006	0.026
	Nov	0.085	0.042	0.006	0.003	0.017	0.169	0.089	0.008	0.004	0.027
	Dec	0.117	0.066	0.008	0.004	0.019	0.347	0.195	0.036	0.019	0.058
1992	Jan	0.212	0.122	0.016	0.008	0.029	0.508	0.301	0.053	0.031	0.088
	Feb	0.506	0.306	0.049	0.028	0.057	0.685	0.425	0.083	0.039	0.115
	Mar	0.395	0.241	0.046	0.019	0.052	0.565	0.339	0.069	0.029	0.086
	Apr	0.588	0.361	0.084	0.029	0.059	0.377	0.246	0.046	0.017	0.048
	May	0.450	0.275	0.062	0.021	0.058	0.381	0.247	0.049	0.019	0.050
	Jun	0.307	0.189	0.038	0.015	0.036	0.203	0.114	0.012	0.005	0.032
	Jul	0.270	0.173	0.032	0.010	0.031	0.272	0.163	0.035	0.010	0.033
	Aug	0.408	0.259	0.047	0.013	0.051	0.276	0.165	0.037	0.009	0.029
	Sep	*	*	*	*	*	0.219	0.124	0.023	0.008	0.026
	Oct	0.152	0.085	0.012	0.005	0.021	0.162	0.084	0.012	0.007	0.022
	Nov	0.098	0.054	0.009	0.004	0.022	0.181	0.099	0.015	0.001	0.024
	Dec	0.175	0.096	0.015	0.008	0.025	0.402	0.243	0.052	0.030	0.044
1993	Jan	0.321	0.192	0.036	0.014	0.034	0.602	0.358	0.080	0.043	0.063
	Feb	0.288	0.172	0.030	0.015	0.031	0.271	0.164	0.028	0.016	0.032
	Mar	0.398	0.246	0.062	0.028	0.041	0.412	0.247	0.044	0.023	0.049
	Apr	0.583	0.360	0.092	0.042	0.057	0.386	0.253	0.049	0.021	0.046

Appendix 3.7. Seasonal variations in the percentage composition of biochemical components in the mantle tissue of *Aequipecten opercularis* (65 - 70 mm shell length) from the Laxey Bay and Port St. Mary. Values are % dry weight except for water (% wet weight). (Values represent means for 10 - 15 individuals) * not available

		Mantle tissue (Laxey Bay)				Mantle tissue (Port St. Mary)			
Year	Month	Protein	Lipid	Glycogen	Water	Protein	Lipid	Glycogen	Water
1991	May	63.49	3.61	1.22	87.23	69.40	3.96	1.49	87.61
	Jun	64.94	3.90	1.30	86.93	67.14	3.36	1.06	86.23
	Jul	61.69	4.04	3.43	86.71	65.99	3.26	2.10	88.47
	Aug	65.96	2.98	2.06	87.04	66.50	2.82	3.58	85.03
	Sep	65.08	4.30	3.25	86.60	65.79	3.90	4.69	87.09
	Oct	65.68	3.79	5.22	86.82	65.48	3.35	6.14	86.14
	Nov	63.93	3.41	1.81	87.54	63.13	3.56	3.34	87.36
	Dec	62.51	3.65	1.47	87.40	60.58	3.52	4.16	87.07
1992	Jan	59.39	2.99	1.16	88.25	63.22	3.28	2.18	87.80
	Feb	60.92	3.10	0.91	88.24	66.68	2.95	1.51	87.69
	Mar	61.34	3.16	0.62	88.93	67.91	3.57	0.95	88.36
	Apr	64.09	4.06	1.04	87.99	71.30	3.73	1.49	88.28
	May	64.04	4.03	0.96	87.04	67.93	3.82	1.21	88.59
	Jun	65.63	3.97	1.96	87.29	66.24	3.13	1.12	88.49
	Jul	61.86	3.92	4.16	86.94	61.91	3.57	3.45	87.58
	Aug	62.02	3.87	3.50	86.91	61.98	3.66	3.21	85.74
	Sep	*	*	*	*	61.32	3.50	4.80	85.30
	Oct	60.36	4.22	2.24	86.87	60.98	3.61	6.15	86.56
	Nov	61.20	3.70	3.84	86.63	61.58	3.41	4.83	87.15
	Dec	61.18	3.66	1.47	86.43	59.40	4.34	4.33	86.66
1993	Jan	62.83	4.73	1.02	87.59	61.74	3.46	2.03	88.29
	Feb	62.13	3.76	1.49	87.89	61.59	4.02	2.22	88.27
	Mar	65.08	3.85	2.11	87.73	64.37	4.03	1.84	88.28
	Apr	63.50	4.15	1.97	87.72	68.29	3.93	1.28	88.03

Appendix 3.8. Seasonal variations in the absolute content (in grams) of biochemical components in the mantle tissue of *Aequipecten opercularis* (65 - 70 mm shell length) from the Laxey Bay and Port St. Mary. (Values represent means for 10 - 15 individuals) * not available

		Mantle tissue (Laxey Bay)				Mantle tissue (Port St. Mary)			
Year	Month	Dry wt	Protein	Lipid	Glycogen	Dry wt	Protein	Lipid	Glycogen
1991	May	0.702	0.445	0.025	0.009	0.786	0.545	0.031	0.012
	Jun	0.755	0.490	0.029	0.010	0.687	0.461	0.023	0.007
	Jul	0.779	0.481	0.031	0.027	0.601	0.394	0.019	0.013
	Aug	0.832	0.549	0.025	0.017	0.839	0.558	0.024	0.030
	Sep	0.854	0.556	0.037	0.028	0.940	0.618	0.036	0.044
	Oct	0.882	0.579	0.033	0.046	0.992	0.650	0.033	0.061
	Nov	0.868	0.491	0.026	0.014	1.247	0.787	0.044	0.042
	Dec	0.905	0.566	0.033	0.013	1.079	0.653	0.038	0.045
1992	Jan	0.818	0.486	0.024	0.009	0.883	0.558	0.020	0.019
	Feb	0.764	0.465	0.023	0.007	0.770	0.514	0.023	0.012
	Mar	0.766	0.470	0.024	0.005	0.897	0.609	0.032	0.009
	Apr	0.690	0.442	0.028	0.007	0.800	0.571	0.030	0.012
	May	0.705	0.451	0.028	0.007	0.729	0.495	0.028	0.009
	Jun	0.754	0.495	0.030	0.015	0.865	0.573	0.027	0.009
	Jul	0.779	0.482	0.031	0.032	0.851	0.527	0.030	0.029
	Aug	0.865	0.536	0.033	0.030	0.905	0.561	0.033	0.029
	Sep	*	*	*	*	0.895	0.549	0.031	0.043
	Oct	0.923	0.557	0.039	0.021	0.870	0.531	0.032	0.054
	Nov	0.868	0.531	0.032	0.033	0.862	0.531	0.029	0.041
	Dec	0.834	0.510	0.030	0.012	0.806	0.479	0.036	0.035
1993	Jan	0.778	0.489	0.037	0.008	0.747	0.461	0.026	0.015
	Feb	0.677	0.420	0.025	0.011	0.709	0.436	0.028	0.016
	Mar	0.719	0.468	0.028	0.015	0.659	0.421	0.027	0.012
	Apr	0.755	0.480	0.031	0.015	0.720	0.492	0.028	0.009

Appendix 3.9. Seasonal variations in the percentage composition of biochemical components in the digestive gland of *Aequipecten opercularis* (65 - 70 mm shell length) from the Laxey Bay and Port St. Mary. Values are % dry weight except for water (% wet weight). * not available ** ash (mantle, gill and digestive gland)

		Digestive gland (Laxey Bay)					Digestive gland (Port St. Mary)				
Year	Month	Protein	Lipid	Glycogen	**Ash	Water	Protein	Lipid	Glycogen	**Ash	Water
1991	May	44.30	5.32	6.54	14.21	74.78	53.21	7.42	6.34	18.00	75.52
	Jun	37.39	8.98	6.55	15.55	74.80	48.49	5.62	9.37	19.63	74.40
	Jul	33.41	20.01	4.43	15.49	73.13	43.20	9.60	5.80	20.63	73.49
	Aug	35.27	25.06	5.42	14.91	72.83	32.16	15.81	2.49	15.75	69.60
	Sep	36.62	22.04	7.26	16.06	71.38	29.75	19.92	3.19	15.62	72.82
	Oct	24.57	23.76	3.47	17.15	69.93	24.94	26.58	4.15	14.43	69.46
	Nov	32.76	29.62	6.02	17.29	72.95	27.47	27.16	5.12	16.17	71.57
	Dec	32.74	24.58	6.68	17.44	73.37	27.04	14.15	6.25	17.27	70.57
1992	Jan	31.12	16.71	5.35	17.62	73.21	26.25	21.28	4.19	16.46	71.26
	Feb	38.61	14.26	7.40	17.74	75.55	32.87	15.25	4.94	17.83	73.23
	Mar	45.66	3.97	8.03	17.56	78.68	44.36	7.23	7.14	14.83	78.81
	Apr	45.23	5.97	7.02	17.19	77.37	51.41	7.29	6.68	16.71	78.80
	May	44.95	5.15	7.29	17.54	76.12	52.20	7.68	5.87	19.00	78.25
	Jun	37.46	9.98	8.21	17.37	74.87	48.19	5.24	10.01	17.44	75.23
	Jul	33.36	20.31	4.30	16.37	70.82	34.34	21.29	4.49	16.04	71.77
	Aug	33.25	20.49	4.65	15.78	71.80	34.76	21.64	4.01	15.51	71.63
	Sep	*	*	*	*	*	30.06	25.50	5.30	14.44	70.50
	Oct	25.16	33.20	5.83	15.30	70.69	25.22	33.10	6.71	14.94	68.49
	Nov	22.70	33.05	2.08	15.26	71.70	27.07	33.64	6.36	17.26	71.48
	Dec	22.70	33.65	2.06	15.15	72.21	22.90	30.48	2.69	15.48	71.82
1993	Jan	32.93	10.06	3.35	15.19	72.79	30.26	12.14	6.26	15.05	73.50
	Feb	32.43	11.24	6.69	16.25	71.55	37.19	7.35	7.36	18.86	77.01
	Mar	46.65	5.71	9.95	18.87	77.18	36.82	7.57	6.76	20.51	77.12
	Apr	45.63	5.84	9.98	19.42	77.21	51.47	7.54	6.02	19.82	78.05

Appendix 3.10. Seasonal variations in the absolute content (in grams) of biochemical components in the digestive gland of *Aequipecten opercularis* (65 - 70 mm shell length) from the Laxey Bay and Port St. Mary. (Values represent means for 10 - 15 individuals) * not available ** ash (mantle, gill and digestive gland)

		Digestive gland (Laxey Bay)					Digestive gland (Port St. Mary)				
Year	Month	Dry wt	Protein	Lipid	Glycogen	**Ash	Dry wt	Protein	Lipid	Glycogen	**Ash
1991	May	0.214	0.095	0.011	0.014	0.134	0.256	0.136	0.019	0.016	0.187
	Jun	0.279	0.104	0.025	0.018	0.161	0.363	0.176	0.020	0.034	0.206
	Jul	0.335	0.112	0.067	0.015	0.173	0.408	0.176	0.039	0.024	0.208
	Aug	0.320	0.113	0.080	0.017	0.172	0.546	0.175	0.086	0.014	0.218
	Sep	0.334	0.122	0.074	0.024	0.191	0.526	0.157	0.105	0.017	0.229
	Oct	0.343	0.084	0.081	0.012	0.210	0.556	0.139	0.148	0.023	0.223
	Nov	0.277	0.091	0.082	0.017	0.207	0.387	0.106	0.105	0.020	0.264
	Dec	0.266	0.087	0.065	0.018	0.204	0.378	0.102	0.053	0.024	0.251
1992	Jan	0.246	0.077	0.041	0.013	0.188	0.344	0.090	0.073	0.014	0.202
	Feb	0.212	0.082	0.030	0.016	0.173	0.317	0.104	0.048	0.016	0.194
	Mar	0.202	0.092	0.008	0.016	0.170	0.232	0.103	0.017	0.017	0.167
	Apr	0.205	0.093	0.012	0.014	0.154	0.246	0.126	0.018	0.016	0.175
	May	0.245	0.110	0.013	0.018	0.167	0.256	0.133	0.020	0.015	0.187
	Jun	0.285	0.107	0.028	0.023	0.180	0.224	0.108	0.012	0.022	0.190
	Jul	0.331	0.110	0.067	0.014	0.182	0.359	0.123	0.076	0.016	0.194
	Aug	0.361	0.120	0.074	0.017	0.193	0.379	0.132	0.082	0.015	0.199
	Sep	*	*	*	*	*	0.390	0.117	0.100	0.021	0.186
	Oct	0.428	0.108	0.142	0.025	0.207	0.417	0.105	0.138	0.028	0.192
	Nov	0.408	0.093	0.135	0.008	0.195	0.309	0.084	0.104	0.020	0.202
	Dec	0.369	0.084	0.124	0.008	0.182	0.368	0.084	0.112	0.010	0.182
1993	Jan	0.216	0.071	0.022	0.007	0.151	0.309	0.093	0.037	0.019	0.159
	Feb	0.239	0.077	0.027	0.016	0.149	0.226	0.084	0.017	0.017	0.176
	Mar	0.213	0.099	0.012	0.021	0.180	0.207	0.076	0.016	0.014	0.178
	Apr	0.230	0.105	0.013	0.023	0.191	0.224	0.115	0.017	0.013	0.187

Appendix 3.11. Seasonal variations in the percentage composition of biochemical components in the adductor muscle of *Pecten maximus* (120 - 130 mm shell length) from the Laxey Bay and Port St. Mary. Values are % dry weight except for water (% wet weight). (Values represent means for 10 - 15 individuals)

		Adductor muscle (Laxey Bay)					Adductor muscle (Port St. Mary)				
Year	Month	Protein	Lipid	Glycogen	Ash	Water	Protein	Lipid	Glycogen	Ash	Water
1991	May	75.09	2.68	6.28	6.57	75.74	71.71	2.67	7.93	8.03	77.21
	Jun	72.46	2.85	9.29	9.38	75.66	70.30	2.24	7.36	7.85	76.73
	Jul	70.89	2.73	5.76	9.82	75.33	72.73	2.83	6.63	8.36	77.69
	Aug	75.41	2.78	5.75	7.18	74.99	67.54	2.83	11.18	8.52	75.98
	Sep	75.58	3.58	11.32	9.16	75.06	72.26	2.95	9.47	12.51	74.99
	Oct	66.61	3.28	15.89	12.96	74.99	65.62	3.41	14.79	7.39	74.48
	Nov	64.77	3.39	10.59	10.31	74.77	61.73	2.73	14.40	8.13	75.34
	Dec	65.28	2.78	15.01	6.81	74.92	60.02	2.63	14.19	8.30	75.46
1992	Jan	70.41	3.37	9.47	8.54	76.33	62.67	3.00	13.04	8.91	75.74
	Feb	68.36	2.88	10.51	10.10	77.19	65.83	2.74	14.52	9.06	76.80
	Mar	76.22	3.14	6.09	11.06	78.82	74.17	3.03	7.13	8.12	77.03
	Apr	76.08	2.78	7.03	8.52	78.11	73.69	2.62	7.13	8.15	77.96
	May	75.26	2.78	7.66	9.10	75.72	73.28	2.53	7.48	8.11	77.73
	Jun	72.43	2.91	9.54	9.67	77.06	73.49	2.90	8.59	8.15	77.78
	Jul	67.92	2.82	14.38	7.95	75.47	63.57	2.67	15.52	6.25	75.15
	Aug	69.11	2.80	14.01	9.63	75.84	62.34	2.59	15.10	8.05	75.20
	Sep	65.36	2.71	14.67	10.84	74.98	63.12	2.79	14.80	10.08	75.11
	Oct	62.14	2.82	15.55	12.95	74.13	64.26	2.96	12.53	10.89	75.02
	Nov	64.72	3.02	16.18	10.33	74.74	69.39	3.08	15.05	10.82	75.45
	Dec	63.30	3.31	15.29	7.15	74.52	67.33	3.02	14.63	11.32	76.18
1993	Jan	67.74	3.10	15.36	8.20	76.30	71.70	2.75	11.26	7.47	77.26
	Feb	70.62	3.04	13.98	6.93	76.88	72.94	2.98	6.64	9.60	78.10
	Mar	73.35	3.10	12.35	7.10	77.24	74.03	3.32	6.87	7.38	77.42
	Apr	73.15	3.03	11.86	7.49	77.55	73.42	2.85	8.09	7.81	77.30

Appendix 3.12. Seasonal variations in the absolute content (in grams) of biochemical components in the adductor muscle of *Pecten maximus* (120 - 130 mm shell length) from the Laxey Bay and Port St. Mary. (Values represent means for 10 - 15 individuals)

		Adductor muscle (Laxey Bay)					Adductor muscle (Port St. Mary)				
Year	Month	Dry wt.	Protein	Lipid	Glycogen	Ash	Dry wt.	Protein	Lipid	Glycogen	Ash
1991	May	7.426	5.576	0.199	0.466	0.488	6.852	4.914	0.183	0.543	0.550
	Jun	7.363	5.335	0.210	0.684	0.690	7.340	5.160	0.164	0.540	0.576
	Jul	7.596	5.384	0.207	0.438	0.746	6.782	4.933	0.192	0.450	0.567
	Aug	7.705	5.810	0.214	0.443	0.553	7.661	5.174	0.217	0.857	0.653
	Sep	8.217	6.210	0.294	0.930	0.753	5.514	6.152	0.251	0.806	0.745
	Oct	8.121	5.409	0.266	1.290	1.052	9.339	6.128	0.318	1.381	0.690
	Nov	8.976	5.813	0.304	0.951	0.925	9.171	5.661	0.250	1.321	0.746
	Dec	8.095	5.284	0.225	1.215	0.552	8.577	5.148	0.256	1.217	0.712
1992	Jan	7.264	5.115	0.245	0.689	0.620	8.147	5.106	0.244	1.062	0.726
	Feb	6.820	4.662	0.196	0.717	0.689	7.106	4.678	0.195	1.032	0.644
	Mar	6.361	4.848	0.200	0.387	0.704	7.087	5.256	0.215	0.505	0.576
	Apr	6.286	4.783	0.175	0.442	0.535	6.632	4.887	0.174	0.473	0.541
	May	6.356	4.784	0.177	0.487	0.578	6.454	4.729	0.163	0.483	0.523
	Jun	6.427	4.655	0.187	0.613	0.622	6.783	4.985	0.197	0.583	0.553
	Jul	7.273	4.940	0.205	1.046	0.578	8.394	5.336	0.224	1.303	0.525
	Aug	6.949	4.802	0.195	0.974	0.669	8.381	5.225	0.217	1.266	0.675
	Sep	7.826	5.115	0.212	1.148	0.848	8.464	5.343	0.236	1.253	0.853
	Oct	8.705	5.409	0.245	1.354	1.127	8.546	5.492	0.253	1.071	0.931
	Nov	8.842	5.724	0.267	1.430	0.913	7.977	5.535	0.246	1.201	0.863
	Dec	8.627	5.460	0.286	1.319	0.617	7.004	4.716	0.212	1.025	0.793
1993	Jan	7.446	5.044	0.231	1.144	0.611	7.020	5.034	0.193	0.790	0.524
	Feb	6.671	4.711	0.203	0.933	0.463	6.657	4.856	0.198	0.442	0.639
	Mar	6.001	4.402	0.186	0.741	0.426	6.627	4.906	0.220	0.455	0.489
	Apr	6.086	4.452	0.184	0.722	0.456	6.749	4.955	0.192	0.546	0.527

Appendix 3.13. Seasonal variations in the percentage composition of biochemical components in the testis of *Pecten maximus* (120 - 130 mm shell length) from the Laxey Bay and Port St. Mary. Values are % dry weight. (Values represent means for 10 - 15 individuals)

		Testis (Laxey Bay)			Testis (Port. St. Mary)		
Year	Month	Protein	Lipid	Glycogen	Protein	Lipid	Glycogen
1991	May	74.10	5.09	4.78	72.67	5.73	3.79
	Jun	67.68	5.17	5.19	73.83	6.14	4.09
	Jul	71.91	5.10	3.62	74.72	5.19	3.49
	Aug	64.71	4.96	3.76	61.18	3.76	1.73
	Sep	71.04	6.20	2.98	65.15	5.77	1.86
	Oct	58.46	6.21	4.79	65.15	5.04	3.22
	Nov	72.11	6.42	5.57	66.79	5.20	4.39
	Dec	69.45	5.33	5.02	70.00	6.01	4.53
1992	Jan	69.80	6.38	4.27	72.33	6.25	4.92
	Feb	71.78	5.98	5.67	69.73	5.57	5.40
	Mar	74.31	6.22	4.50	74.24	6.10	4.69
	Apr	74.99	5.20	4.83	73.21	5.69	4.67
	May	75.26	4.78	5.66	73.21	5.92	3.96
	Jun	69.76	5.11	4.85	74.03	6.62	4.99
	Jul	65.68	6.29	4.71	61.18	4.76	4.94
	Aug	63.51	6.39	4.36	60.09	4.79	4.83
	Sep	65.18	6.51	4.57	65.62	5.93	5.94
	Oct	66.51	7.00	5.10	68.72	6.28	6.71
	Nov	67.61	8.16	6.22	69.66	8.14	7.98
	Dec	68.84	7.38	5.98	73.01	8.72	6.75
1993	Jan	71.37	7.25	6.50	69.52	6.49	7.44
	Feb	73.90	7.37	6.67	71.37	6.61	7.22
	Mar	76.08	7.00	6.76	72.12	6.34	6.83
	Apr	71.85	6.94	6.35	72.80	5.36	4.16

Appendix 3.14. Seasonal variations in the percentage composition of biochemical components in the ovary of *Pecten* maximus (120 - 130 mm shell length) from the Laxey Bay and Port St. Mary. Values are % dry weight. (Values represent means for 10 - 15 individuals)

		Ovary (Laxey Bay)			Ovary (Port. St. Mary)		
Year	Month	Protein	Lipid	Glycogen	Protein	Lipid	Glycogen
1991	May	56.11	12.52	5.78	54.35	12.37	4.21
	Jun	51.48	11.26	6.05	54.36	12.65	6.18
	Jul	55.17	12.27	3.29	56.67	12.39	3.27
	Aug	56.33	12.22	3.74	50.18	5.66	2.36
	Sep	54.31	8.54	3.25	50.52	9.13	5.25
	Oct	50.91	8.21	5.60	51.89	8.69	5.20
	Nov	52.42	9.90	7.57	51.48	14.60	6.11
	Dec	52.16	11.09	6.99	51.13	14.21	6.35
1992	Jan	51.95	12.26	5.09	50.49	12.22	6.02
	Feb	50.24	9.32	5.66	50.24	7.29	4.90
	Mar	53.39	13.92	4.40	51.75	10.34	4.56
	Apr	54.48	12.49	5.97	54.07	15.23	4.36
	May	55.10	12.42	5.24	54.14	12.23	4.12
	Jun	52.20	10.88	5.11	52.36	14.63	6.45
	Jul	51.46	9.52	6.13	49.56	7.10	6.27
	Aug	51.34	8.88	6.30	49.83	7.43	5.84
	Sep	53.60	9.86	6.20	51.31	11.30	7.70
	Oct	54.89	9.11	5.77	51.68	13.36	7.93
	Nov	51.06	13.26	7.77	49.84	13.22	9.54
	Dec	50.86	13.30	7.62	54.14	18.02	8.74
1993	Jan	53.80	15.35	5.92	51.06	16.64	8.94
	Feb	51.13	12.09	7.28	52.91	14.70	5.27
	Mar	54.62	9.82	6.46	52.02	12.08	4.74
	Apr	53.39	9.96	6.60	54.21	11.78	4.14

Appendix 3.15. Seasonal variations in the percentage composition of biochemical components in the total gonad (testis and ovary combined) of *Pecten maximus* (120 - 130 mm shell length) from the Laxey Bay and Port St. Mary. Values are % dry weight except for water (% wet weight). (Values represent means for 10 - 15 individuals)

		Total gonad (Laxey Bay)					Total gonad (Port St. Mary)				
Year	Month	Protein	Lipid	Glycogen	Ash	Water	Protein	Lipid	Glycogen	Ash	Water
1991	May	65.10	8.81	5.28	17.28	76.77	63.51	9.05	4.00	17.98	79.35
	Jun	59.58	8.22	5.62	23.62	82.17	64.09	9.40	5.14	19.68	80.06
	Jul	63.54	8.68	3.46	15.80	82.74	65.69	9.29	3.38	19.97	81.45
	Aug	60.52	8.59	3.75	12.92	80.74	55.68	4.71	2.05	20.34	85.35
	Sep	62.67	7.37	3.11	13.44	82.78	57.83	7.45	3.56	14.30	82.70
	Oct	54.69	7.21	5.20	16.79	83.85	58.52	6.86	4.21	13.08	82.33
	Nov	62.26	8.16	6.57	13.72	80.33	59.14	9.90	5.25	12.98	81.60
	Dec	60.80	8.21	6.01	12.60	81.26	60.57	10.11	5.44	13.25	79.19
1992	Jan	60.87	9.32	4.68	14.18	80.12	61.41	9.23	5.47	13.35	77.31
	Feb	61.01	7.65	5.66	12.85	78.75	59.98	6.43	5.15	13.37	78.87
	Mar	63.85	10.07	4.45	15.94	79.09	62.99	8.22	4.62	11.86	77.67
	Apr	64.73	8.85	5.40	12.69	78.48	63.64	10.46	4.52	11.85	77.55
	May	65.18	8.60	5.45	10.01	77.21	63.67	9.08	4.04	12.25	78.50
	Jun	60.98	7.99	4.98	14.22	81.29	63.20	10.62	5.72	12.92	79.39
	Jul	58.57	7.91	5.42	13.81	81.12	55.37	5.93	5.61	14.71	83.28
	Aug	57.42	7.64	5.33	13.78	81.38	54.96	6.11	5.33	17.53	84.13
	Sep	59.39	8.19	5.39	14.97	82.67	58.46	8.61	6.82	16.94	82.34
	Oct	60.70	8.06	5.43	17.85	83.97	60.22	9.82	7.32	16.70	80.54
	Nov	59.34	10.71	6.99	14.06	80.36	59.75	10.68	8.76	14.38	79.84
	Dec	59.85	10.34	6.80	15.20	83.08	63.57	13.37	7.75	13.49	79.55
1993	Jan	62.59	11.30	6.21	12.67	79.95	60.29	11.56	8.19	11.37	78.35
	Feb	62.52	9.73	6.97	12.57	80.59	62.14	10.66	6.25	11.54	78.97
	Mar	65.35	8.41	6.61	11.93	79.30	62.07	9.21	5.79	11.10	78.04
	Apr	62.62	8.45	6.48	12.27	78.86	63.51	8.57	4.15	11.23	77.94

Appendix 3.16. Seasonal variations in the absolute content (in grams) of biochemical components in the total gonad (testis and ovary) of *Pecten maximus* (120 - 130 mm shell length) from the Laxey Bay and Port St. Mary. (Values represent means for 10 - 15 individuals)

		Total gonad (Laxey Bay)					Total gonad (Port St. Mary)				
Year	Month	Dry wt.	Protein	Lipid	Glycogen	Ash	Dry wt.	Protein	Lipid	Glycogen	Ash
1991	May	3.517	2.290	0.310	0.186	0.608	3.065	1.947	0.277	0.123	0.551
	Jun	2.280	1.358	0.187	0.128	0.539	2.147	1.376	0.203	0.110	0.423
	Jul	1.137	0.722	0.099	0.039	0.180	1.447	0.951	0.134	0.049	0.289
	Aug	1.513	0.916	0.130	0.057	0.196	0.702	0.391	0.033	0.014	0.143
	Sep	1.068	0.669	0.079	0.033	0.144	0.872	0.504	0.065	0.030	0.125
	Oct	0.581	0.318	0.042	0.030	0.098	0.916	0.536	0.063	0.039	0.120
	Nov	1.276	0.795	0.104	0.084	0.175	1.445	0.855	0.143	0.076	0.188
	Dec	1.311	0.797	0.108	0.079	0.165	2.412	1.461	0.244	0.131	0.320
1992	Jan	1.461	0.889	0.136	0.068	0.207	3.390	2.082	0.313	0.185	0.453
	Feb	3.614	2.205	0.274	0.205	0.465	2.940	1.764	0.189	0.151	0.393
	Mar	3.473	2.218	0.350	0.155	0.554	4.223	2.660	0.347	0.195	0.501
	Apr	3.509	2.271	0.310	0.189	0.445	4.692	2.986	0.491	0.211	0.556
	May	3.245	2.115	0.279	0.177	0.325	4.276	2.723	0.388	0.173	0.524
	Jun	1.440	0.878	0.115	0.072	0.205	4.149	2.622	0.441	0.237	0.536
	Jul	1.413	0.828	0.112	0.077	0.195	1.049	0.581	0.062	0.058	0.154
	Aug	1.350	0.775	0.103	0.072	0.186	0.887	0.488	0.054	0.047	0.156
	Sep	0.955	0.567	0.078	0.051	0.143	1.560	0.912	0.134	0.106	0.264
	Oct	0.559	0.339	0.045	0.030	0.099	2.234	1.345	0.219	0.164	0.373
	Nov	1.256	0.745	0.135	0.088	0.177	2.339	1.398	0.250	0.205	0.337
	Dec	1.009	0.604	0.104	0.069	0.153	2.284	1.452	0.305	0.177	0.308
1993	Jan	2.086	1.306	0.236	0.130	0.264	3.792	2.286	0.439	0.311	0.431
	Feb	2.342	1.464	0.228	0.163	0.295	3.580	2.225	0.381	0.224	0.413
	Mar	2.235	1.461	0.188	0.148	0.267	3.559	2.209	0.328	0.206	0.395
	Apr	3.043	1.906	0.257	0.197	0.373	3.873	2.460	0.332	0.161	0.435

Appendix 3.17. Seasonal variations in the percentage composition of biochemical components in the mantle tissue of *Pecten maximus* (120 - 130 mm shell length) from the Laxey Bay and Port St. Mary. Values are % dry weight except for water (% wet weight). (Values represent means for 10 - 15 individuals)

		Mantle tissue (Laxey Bay)				Mantle tissue (Port St. Mary)			
Year	Month	Protein	Lipid	Glycogen	Water	Protein	Lipid	Glycogen	Water
1991	May	59.61	2.74	1.42	89.21	58.09	2.82	1.33	89.51
	Jun	60.64	2.90	2.22	89.07	58.55	3.24	1.09	89.11
	Jul	65.28	2.72	0.98	88.64	64.05	2.72	0.99	88.47
	Aug	63.50	2.83	1.21	88.32	59.95	2.60	1.28	89.29
	Sep	62.66	2.78	0.74	88.56	60.02	2.24	1.88	88.18
	Oct	63.06	2.70	1.41	88.30	60.83	2.99	3.72	88.00
	Nov	61.95	2.99	1.36	88.89	58.65	2.57	1.43	88.64
	Dec	59.13	2.62	1.71	89.92	58.04	2.62	1.49	89.26
1992	Jan	60.43	3.15	1.36	90.09	58.46	3.04	1.43	89.56
	Feb	64.94	2.80	1.43	89.43	62.48	2.73	1.53	89.69
	Mar	62.61	3.28	1.02	89.99	60.77	2.87	1.43	88.74
	Apr	60.02	3.39	1.51	89.06	61.28	2.78	1.29	89.16
	May	60.09	2.92	1.44	88.71	60.50	2.91	1.28	89.02
	Jun	60.89	2.82	1.30	88.65	59.35	3.07	1.15	89.21
	Jul	62.62	2.97	2.20	88.99	61.39	2.95	2.64	89.59
	Aug	61.72	2.96	1.81	88.75	61.05	3.01	2.50	89.21
	Sep	60.15	3.20	1.61	88.32	60.55	3.31	2.54	89.33
	Oct	59.06	3.19	1.50	89.07	58.58	3.48	2.11	89.50
	Nov	58.04	3.58	3.23	89.47	56.53	3.77	2.37	90.30
	Dec	56.26	3.51	2.12	89.91	59.95	3.86	2.74	89.71
1993	Jan	59.40	3.44	2.66	89.33	59.27	3.28	2.38	89.29
	Feb	63.37	3.42	2.15	90.52	61.52	3.77	2.02	89.92
	Mar	61.93	3.35	1.26	90.10	60.36	3.66	2.52	89.72
	Apr	61.04	3.33	1.34	89.80	59.20	2.83	1.28	89.24

Appendix 3.18. Seasonal variations in the absolute content (in grams) of biochemical components in the mantle tissue of *Pecten maximus* (120 - 130 mm shell length) from the Laxey Bay and Port St. Mary. (Values represent means for 10 - 15 individuals)

		Mantle tissue (Laxey Bay)				Mantle tissue (Port St. Mary)			
Year	Month	Dry wt.	Protein	Lipid	Glycogen	Dry wt.	Protein	Lipid	Glycogen
1991	May	2.673	1.593	0.073	0.038	3.136	1.822	0.089	0.042
	Jun	3.410	2.068	0.098	0.076	3.006	1.760	0.097	0.033
	Jul	3.175	2.072	0.086	0.031	2.602	1.667	0.071	0.026
	Aug	3.048	1.935	0.086	0.037	2.449	1.468	0.064	0.031
	Sep	3.142	1.969	0.087	0.023	2.598	1.559	0.058	0.049
	Oct	3.194	2.014	0.086	0.045	2.817	1.714	0.084	0.105
	Nov	3.222	1.996	0.096	0.044	3.033	1.779	0.078	0.043
	Dec	2.882	1.704	0.076	0.049	2.983	1.731	0.078	0.044
1992	Jan	2.828	1.709	0.089	0.038	3.116	1.822	0.095	0.045
	Feb	2.812	1.826	0.079	0.040	2.548	1.592	0.070	0.039
	Mar	2.966	1.857	0.097	0.030	2.678	1.627	0.077	0.038
	Apr	3.045	1.829	0.103	0.046	2.704	1.657	0.075	0.035
	May	2.848	1.711	0.083	0.041	2.625	1.588	0.076	0.034
	Jun	3.089	1.880	0.087	0.040	2.879	1.709	0.088	0.033
	Jul	3.209	2.009	0.095	0.071	2.673	1.641	0.079	0.071
	Aug	3.209	1.981	0.094	0.058	2.738	1.672	0.082	0.068
	Sep	3.258	1.960	0.104	0.052	2.665	1.614	0.088	0.067
	Oct	3.416	2.017	0.109	0.051	2.581	1.512	0.090	0.054
	Nov	3.151	1.829	0.113	0.102	3.091	1.747	0.117	0.073
	Dec	3.306	1.860	0.116	0.070	2.982	1.789	0.115	0.082
1993	Jan	3.033	1.802	0.104	0.081	3.213	1.904	0.105	0.076
	Feb	3.013	1.909	0.103	0.065	2.840	1.747	0.107	0.057
	Mar	3.212	1.989	0.108	0.041	3.126	1.887	0.114	0.079
	Apr	2.986	1.823	0.099	0.040	3.230	1.912	0.091	0.041

Appendix 3.19. Seasonal variations in the percentage composition of biochemical components in the digestive gland of *Pecten maximus* (120 - 130 mm shell length) from the Laxey Bay and Port St. Mary. Values are % dry weight except for water (% wet weight). (Values represent means for 10 - 15 individuals) ** ash (mantle, gill and digestive gland)

		Digestive gland (Laxey Bay)					Digestive gland (Port St. Mary)				
Year	Month	Protein	Lipid	Glycogen	**Ash	Water	Protein	Lipid	Glycogen	**Ash	Water
1991	May	48.13	13.07	10.54	19.67	75.65	41.90	11.40	10.93	25.94	76.45
	Jun	42.99	17.22	10.62	17.78	74.80	43.98	8.61	12.05	26.18	76.25
	Jul	46.21	13.06	10.18	20.43	75.21	47.17	13.25	11.09	23.63	75.72
	Aug	47.58	14.58	9.99	18.08	74.54	38.28	17.25	6.73	22.72	70.29
	Sep	45.66	25.51	11.60	17.87	74.66	31.51	19.19	4.95	17.62	68.96
	Oct	36.70	29.34	9.11	20.43	72.52	35.68	19.81	10.62	18.95	71.84
	Nov	34.30	14.98	8.95	20.92	70.21	28.10	22.01	10.90	21.14	70.08
	Dec	31.79	09.71	11.13	22.21	74.11	27.69	23.24	9.82	21.68	72.22
1992	Jan	33.77	14.04	12.26	20.58	73.89	37.24	9.97	10.17	22.23	73.19
	Feb	32.80	10.30	7.28	22.06	74.72	37.94	11.57	8.38	21.76	76.26
	Mar	41.22	10.15	9.97	22.31	77.27	44.23	13.83	10.44	22.09	76.69
	Apr	45.05	12.20	10.80	22.35	76.87	45.94	11.58	10.80	22.41	77.97
	May	47.10	13.02	9.47	23.48	76.53	45.39	12.24	10.10	21.62	77.52
	Jun	42.17	14.98	11.07	21.58	76.36	45.46	15.43	11.03	19.85	73.37
	Jul	33.25	25.40	9.92	20.85	73.30	37.19	23.07	13.61	17.42	71.19
	Aug	33.70	25.59	9.43	21.56	72.54	37.20	21.92	13.00	19.43	70.50
	Sep	29.35	29.30	9.38	19.96	70.22	32.75	22.64	13.41	18.94	69.23
	Oct	26.87	34.17	9.63	19.79	71.21	28.51	23.41	11.69	18.41	70.09
	Nov	24.68	30.34	10.14	21.28	72.54	31.79	23.33	12.28	20.10	72.47
	Dec	30.76	24.40	9.52	19.92	73.77	28.04	23.61	6.98	21.22	73.36
1993	Jan	34.39	22.70	13.72	22.07	72.57	37.60	20.70	9.68	20.73	77.11
	Feb	38.35	18.65	12.02	22.50	72.75	46.01	9.95	10.70	23.39	78.48
	Mar	41.36	15.22	11.04	24.91	75.69	44.23	9.39	14.00	25.21	78.62
	Apr	38.62	13.58	11.16	24.83	75.80	45.12	11.40	11.10	25.20	77.12

Appendix 3.20. Seasonal variations in the absolute content (in grams) of biochemical components in the digestive gland of *Pecten maximus* (120 - 130 mm shell length) from the Laxey Bay and Port St. Mary. (Values represent means for 10 - 15 individuals) ** ash (mantle, gill and digestive gland)

		Digestive gland (Laxey Bay)					Digestive gland (Port St. Mary)				
Year	Month	Dry wt.	Protein	Lipid	Glycogen	**Ash	Dry wt.	Protein	Lipid	Glycogen	** Ash
1991	May	1.132	0.545	0.148	0.119	0.749	1.365	0.572	0.156	0.149	1.168
	Jun	1.251	0.538	0.215	0.133	0.828	1.628	0.716	0.140	0.196	1.213
	Jul	1.270	0.587	0.166	0.129	0.908	2.209	1.042	0.293	0.245	1.137
	Aug	1.450	0.690	0.211	0.145	0.813	2.220	0.850	0.383	0.149	1.061
	Sep	1.516	0.692	0.387	0.176	0.833	1.902	0.599	0.365	0.094	0.793
	Oct	1.660	0.609	0.487	0.151	0.992	1.858	0.663	0.368	0.197	0.886
	Nov	1.600	0.549	0.239	0.143	1.008	1.592	0.447	0.350	0.175	0.978
	Dec	1.412	0.449	0.137	0.157	0.954	1.495	0.414	0.347	0.147	0.971
1992	Jan	0.955	0.323	0.134	0.118	0.778	1.211	0.451	0.121	0.123	0.962
	Feb	1.005	0.330	0.104	0.073	0.842	1.073	0.407	0.124	0.089	0.788
	Mar	1.053	0.434	0.107	0.105	0.897	1.052	0.465	0.145	0.109	0.824
	Apr	1.005	0.453	0.123	0.108	0.905	1.134	0.521	0.131	0.122	0.860
	May	1.109	0.523	0.144	0.105	0.929	1.250	0.567	0.153	0.126	0.838
	Jun	1.235	0.521	0.185	0.137	0.933	1.433	0.651	0.221	0.158	0.856
	Jul	1.214	0.404	0.308	0.120	0.922	2.343	0.871	0.541	0.318	0.874
	Aug	1.206	0.406	0.309	0.114	0.951	2.125	0.790	0.465	0.276	0.945
	Sep	1.398	0.410	0.410	0.131	0.930	1.963	0.643	0.444	0.263	0.877
	Oct	1.486	0.399	0.508	0.143	0.970	1.812	0.517	0.424	0.212	0.809
	Nov	1.598	0.394	0.485	0.162	1.011	1.236	0.393	0.288	0.152	0.870
	Dec	1.162	0.357	0.284	0.111	0.890	1.188	0.333	0.280	0.083	0.885
1993	Jan	1.064	0.366	0.242	0.146	0.904	0.910	0.342	0.188	0.088	0.855
	Feb	1.132	0.434	0.211	0.136	0.933	0.689	0.317	0.069	0.074	0.826
	Mar	0.945	0.391	0.144	0.104	1.035	0.643	0.284	0.060	0.090	0.951
	Apr	1.112	0.429	0.151	0.124	1.017	0.920	0.415	0.104	0.102	1.046