GROWTH AND REPRODUCTION OF MYTILUS EDULIS LINNAEUS ON THE TWO SIDES OF THE STRAIT OF BELLE ISLE

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GROWTH AND REPRODUCTION OF MYTILUS EDULIS (LINNAEUS) ON THE TWO SIDES OF THE STRAIT OF BELLE ISLE.

BY

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ABSTRACT

A comparative growth study of Strait of Belle Isle Mytilus edulis populations was undertaken, with the hypothesis that the surface water temperature difference between the two sides of the Strait (4-8 C) results in differences in growth rates. Results of the study show that Mytilus edulis collected at four sites, (two on each side of the Strait) from the high, low, and subtidal zones, displays the type of spawning, growth, and population structure, typical of north-temperate, exposed-coast mussel populations. Linear shell growth rates were similar between the two sides of the Strait. Growth rates were low (maximum of 6-8 mm per year) and were highly variable within populations (average range in length of 10 mm per year class).

Winter growth was negligible as evidenced by pronounced, external shell check-marks, and despite the large spring-summer water temperature difference between sides of the Strait of Belle Isle, the annual spring start of linear shell growth was similar between mussels on the two sides. The seasonal progression of the internal growth line in M. edulis was relatively synchronous within populations, and timing of deposition was similar between sides of the Strait.

Spawning was synchronized and occurred later (July-August) than at more southern latitudes. Subsequent settlement in 1981 resulted in large numbers of post-larvae over-wintering on algae and adult mussel beds at sizes $<$ 2 mm in shell length. There were large differences in fecundity between sites, however, the range in fecundity was similar on both sides of the Strait. Age-specific fecundity was higher in the low intertidal than in the high intertidal (e.g. 160 and 115 mg gamete dry weight respectively, at Pte. Amour).

Mussels < 15 mm in shell length dominated the intertidal zone while contributing little to meat weight biomass. At the sampling scale used in this study (200 cm^2), meat dry weight biomass and reproductive output were similar between high and low intertidal zones. Individual meat weight values were similar between the two sides of the Strait and Pte. Amour meat weight values were highest of those in the intertidal zones while similar to values at other sites subtidally.

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INTRODUCTION

The effect of temperature on metabolism in poikilotherms (e.g. Sparck, 1936; Bullock, 1955; Taylor, 1960; Kinne, 1963; Newell, 1969; Newell and Bayne, 1973), and more specifically on "metabolic rate functions" in Mytilus edulis, has been a subject of considerable interest for many years (Loosanoff, 1942; Widdows and Bayne, 1971; Bayne, 1973; Gabbott and Bayne, 1973; Widdows, 1973). Metabolic rate functions include heart, ventilation and filtration rates, linear shell growth rates and growth of reproductive products. The present thesis compares linear shell growth and reproductive output in populations of the blue mussel (Mytilus edulis) on the two sides of the Strait of Belle Isle.

There is an extensive literature on the differing abilities of poikilotherms to compensate (acclimate) their metabolic rates for differences in temperature. Much of this literature deals with the metabolic rate functions: heart, ventilation and filtration rates (see Hum, 1976). Compensatory adjustment of growth rates to changing temperature, although rare, has been reported previously (Orton, 1923; Dehnel, 1955,1956). Dehnel (1956) reported similar growth rates between Alaskan Mytilus californianus (at 9 C) and Californian M. californianus (at 16 C), however, no latitudinal or seasonal acclimation of linear shell growth rate in mussels was observed by Hum (1976). Linear shell growth rate was greater in mussels from the more southern (warmer water) localities. Bayne and Worrall (1980) identified differences in overall growth rates and fecundity between two mussel populations. These differences were related to differences in temperature and ration between the two sites. In one case, Dehnel (1955) reported higher larval growth rates (including shell growth rate) in northern populations vs. southern populations of several species of gastropods.

In M. edulis, linear shell growth has probably been the most studied metabolic rate function, particularily as a function of temperature, although the influences of other parameters on growth have also been examined (e.g. tidal exposure, wave exposure, light intensity, salinity, food abundance, population density). Although there is an exhaustive literature on growth rates (see Bayne, 1976b), it is often not suitable for comparative purposes as techniques of observation and recording, and subsequent analyses differ (Dehnel, 1955). Since M. edulis has a wide latitudinal distribution (Arctic to North Carolina and to California, Seed, 1976) it must have either excellent thermal acclimation of metabolic rate functions or a wide tolerance of different metabolic levels.

In my study, the oceanographic features of the Strait of Belle Isle afforded the opportunity to compare growth in M. edulis populations over a large temperature difference and a small latitudinal range. Huntsman et al. (1954) report a southwest movement of arctic and sub-arctic water along the north side of the Strait (Labrador and Quebec shores), and a progressive north-easterly movement of warmer Gulf of St. Lawrence water along the south side (Newfoundland shore). Despite the dynamic nature of water flow in the Strait due to variation in meteorological conditions, along with seasonal changes in flow rates (Juszko, 1981), there is a surface water temperature difference (4-8 C) between the two sides of the Strait. In general, surface waters along the north side are in the 29-32‰ salinity range with salinities of 33-34‰ characterizing the south side (Huntsman et al., 1954).

In my study, the question was not whether temperature affects growth rate. Rather, it was of interest to determine, for a relatively sedentary benthic organism such as *M. edulis*, whether or not differences in growth rates (shell growth and growth of soft parts) or in reproduction could be detected within the context of the specific temperature gradient which exists between the two sides of the Strait. I hypothesized that the magnitude of the temperature difference between the two sides of the Strait of Belle Isle should generate differences in linear shell growth rates along with possible differences in reproductive processes (e.g. timing of spawning, fecundity) between the two sides. The study was undertaken to compare growth processes in *M. edulis* from both sides of the Strait of Belle Isle to facilitate a test of my hypothesis.

MATERIALS AND METHODS

FIELD WORK

The Strait of Belle Isle, approximately 118 km in length (Huntsman et al., 1954), separates the island of Newfoundland from Labrador (Fig. 1). The narrowest point is 18 km wide (between Pte. Amour and Savage Cove), afterwhich the Strait widens progressively towards the north to approximately 30 km.

Sampling took place during four field trips in 1981: May 15-22 (limited sampling), June 15-30, August 1-7, and November 17-24. Four sample sites were selected during the May trip, one site from each side of the Strait acting as a replicate. Two were situated on the north shore (Labrador and Quebec), and two on the south shore (Newfoundland). The two north shore sites were Pte. Amour, Labrador (51°27'N, 56°51' W .), and Blanc-Sablon, Quebec (51° 26'N, 57°14'W). The south shore sites were at Anchor Pt., (51°14'N, 56°48'W) and Black Duck Cove (51° 12' N, 56° 48'W). The May field trip was primarily to select sample sites, although limited subtidal sampling was done at Pte. Amour. Intertidal sampling was not possible because of the ice foot still present on shore in mid-May. Quantitative sampling took place in June, August, and November.

An attempt was made to select sites with similar wave exposure and intertidal topography. All four sites are wave exposed rocky shores. The intertidal zones are expansive and gently sloping, with the exception of Anchor Pt., which has a very irregular topography, particularly in the low intertidal. Vertical tidal ranges are on the order of 1.2-1.5 m. The rock at these sites is a mixture of limestone, sandstone, and granite. All sites are structured intertidally by relatively flat rock surfaces, often in ledge arrangements, with sections of rock often meeting at different levels. The relatively flat surfaces are cut in irregular fashion by numerous crevices, particularily at Pte. Amour and Anchor Pt.. Pte. Amour, which has the most extensive intertidal zone along with Blanc-Sablon, has flat rock extending out past the intertidal zone at shallow depths (1-2 meters) for 25 meters, at which point there is a sharp drop to water 3 m in depth.

Blue mussels (Mytilus edulis) were found only at the point where the rock wall and substrate met (angle of junction). At Anchor Pt., in June, the dropoff occurred at the edge of the intertidal zone and blue mussels were again found only within the immediate vicinity, lining the junction created by the rock wall and bottom rock substrate. The intertidal flora at all four sites is generally dominated by summer annuals which re-colonize following ice scouring (Bob Hooper, personal communication). Representative species include Urospora penicilliformis, Chordaria flageliformis and Halosaccion ramentaceum. Fucus spp. persist throughout the year within the intertidal zones.

Both high and low intertidal samples were collected. 'High intertidal' samples were taken at the uppermost limit of mussels on that region of the shore, which was above mid-tide level. Low intertidal samples were collected at approximately the level of mean low water (MLW). Subtidal samples were collected by SCUBA from a depth of approximately 3 m below MLW at Pte. Amour and Anchor Pt., in both June and November, and at Blanc-Sablon in November only. At Anchor Pt., rough sea conditions at the site sampled in June prevented collecting in November; an alternate location was chosen on the protected side of a point approximately 200 m from the June dive location. This area was gently sloping with a cobble/small rock substrate. The depth was approximately 2 m below MLW. In contrast to the other subtidal sites, this area supported a large 'blanket biomass' of blue mussels along with a relatively abundant <u>Asterias/Leptasterias</u> predator population, something not observed at the other exposed sites.

Sampling of <u>Mytilus edulis</u> was usually conducted using a 0.02 m^2 (200 cm^2) quadrat; however, to ensure adequate sample sizes, high intertidal samples from Pte. Amour in June had to be collected without a quadrat. Two replicate samples were collected from each tidal level. Within a given tidal zone mussels living on the seaward side of rock surfaces were collected. Selectivity was necessary because of the heterogenous topography. Mussels were placed in plastic bags on ice and were transferred directly to a laboratory freezer and kept there until analyzed.

The intertidal mussel populations at these sites, particularily at Pte. Amour and Anchor Pt., are predominantly crevice or refuge populations. Because of the dominant influence of ice scour within the intertidal zone mussels exist in relatively dense aggregations within large crevices in the lower intertidal. In areas where wave action is sufficient to provide the lower individuals with aerated water and adequate food, a cluster of mussels up to 25 cm thick can develop. Usually the cluster is anchored to the substratum by the byssus threads of relatively few individuals, with the majority of individuals anchored to each others valves and byssus threads (Dayton, 1971). Aggregations at the Strait sites were usually 10-15 cm in thickness. The mussels collected within these aggregations included specimens from the top, bottom, and middle of clusters and as a result, density-independent growth of top-layer mussels could be obscured by density-dependent growth of bottom mussels. A limited attempt to identify such growth was made through analysis of separate growth of top and bottom mussels.

Surface temperatures at time of sampling were recorded with a mercury thermometer. Limited local temperature/salinity data (July-October 1980) were obtained, courtesy of Brian Petrie, Bedford Institute of Oceanography, from current meters buoyed at 11 m depth on a transect between Savage Cove and Pte. Amour. Average monthly sea surface (i.e. upper 1 m) temperature estimates for Pte. Amour and Savage Cove were obtained from data collected by Bob Hooper, Memorial University, Newfoundland, over a period of several years. In addition, limited thermograph temperature data were collected from the Pte. Amour intertidal zone. In mid-June, two thermographs were placed within the mid intertidal zone, one at Pte. Amour, and the other at Black Duck Cove. On the

August trip a complete thirty-day recording was recovered from Pte. Amour; however, no data were recovered at Black Duck Cove due to an instrument malfunction. The thermograph at Pte. Amour was refitted with recording paper and placed back into position; however, between August and November, it was lost despite a specially constructed anchoring device.

LABORATORY ANALYSIS

Samples of M. edulis were thawed for size-frequency analysis. Samples were first scrutinized with a hand lens to locate any small (< 1 mm) mussels. Representative mussels (6) from size classes were randomly chosen for analysis. Shell length (maximum anterior-posterior distance), shell height (from hinge to opposite ventral surface), and shell width (lateral distance between valves) were measured with vernier calipers to an accuracy of 0.1 mm.

State of the Gonad

The posterior adductor muscle was severed and the shell valves opened to expose the mantle cavity. The macroscopic condition of the mantle tissue was noted for all samples with the aid of a dissecting microscope. A qualitative assessment of the gross reproductive state of the mantle tissue was based upon mantle colouration; and through examination of mantle tissue smears: the presence and extent of coverage of genital follicles, and where possible the degree to which they contained morphologically ripe gametes (i.e. ova 70 microns in diameter: Bayne, 1976a). At the same time, a qualitative assessment was made of the overall condition of the meat (shell-free body mass) using a classification scheme of thick, thin, and very thin. Thick mantles were found in mussels with heavy gamete investment (i.e. pre-spawning). The underlying shell surface in these specimens was not visible. Thin mantles were not necessarily found in post-spawned mussels, however, the mantle was thin enough that the inner shell surface could be detected. Very thin mantles were found in post-spawned mussels and were transparent.

The meat (shell-free body weight) content of each individual mussel was placed on a glass microscope slide and dried at 55 C to constant weight (2 or 3 days). After drying, each slide with meat was weighed to within an accurracy of 0.1 mg, then scraped, washed clean and re-weighed without the meat. The difference was the meat dry weight of individual mussels. Right and left shell valves were air dried and individually weighed to within an accuracy of 10 mg.

Ageing of Mytilus edulis

There are two classical methods of ageing M. edulis. The oldest involves the counting of external, annual growth-interruption marks. These external shell 'check-marks' are caused by periodic changes in linear shell growth rate relative to increase in shell thickness. They have numerous ultimate causes (e.g. rough wave action, spawning, annual winter cessation of growth), and result from the mussel withdrawing its mantle and closing its valves for a period of time. While linear growth has thus ceased temporarily, increase in shell nacre thickness is continuous (Field,1922), so that when favourable growth conditions again exist and the mussel extends its mantle edge and resumes linear shell growth, a discontinuity of pre- and post-disturbance outer shell layers occurs. The result is a ridge or groove with the distinctiveness of the groove depending upon the severity or length of the growth interruption. Mussels in the size range 3-14 mm, too small to section or grind, were observed under a dissecting microscope and distance measurements to external check-marks were made with calipers. In this manner 35 mussels (2.7-9.6 mm) from Pte. Amour and 63 mussels (2.7-13.7 mm) from Black Duck Cove (June, low intertidal samples) were analyzed. The external shell check-marks were placed into two categories: 'well-defined', and 'distinct'. Well-defined check-marks were abrupt changes in shell thickness resulting in sharply delineated grooves, which I suggest were annual, winter growth-interruption marks. 'Distinct' check-marks were not necessarily annual but could also have been spawning or disturbance check- marks, and were not as obvious to the observer.

Mossop (1922) lists the disadvantages associated with the counting of external shell annual check -marks:

(1) Erosion of the shell surface obliterating check-marks.

(2) The difficulty in distinguishing annual (winter) check-marks from other disturbance check-marks.

(3) Crowding of external check-marks at the growing edge in older mussels.

Here, however, these potential problems are minimized. Only young mussels were being investigated, and thus check-marks were neither crowded posteriorly nor worn anteriorly; furthermore, in north temperate mussels, winter check-marks are usually well-defined due to a long winter growth cessation period (Lubinsky, 1958; Theisen, 1973; Wallace, 1980).

The second method of ageing bivalves involves the counting of internal growth lines or bands (Barker, 1964; Pannella and MacClintock, 1968). The formation of the internal growth line in M. edulis has a different cause than external shell-check marks (see APPENDIX A).

Selected mussel shells were aged using a modification of the thin section technique described by Clark (1980). A single shell valve was sectioned with a brass lapidary saw (1 mm blade thickness) beginning at the umbo and cutting through towards the postero-dorso margin. Shells < 15 mm in shell length were ground with sandpaper rather than cut. One edge of the section (dorsal or ventral surface) was smoothed with carborundum polishing grit (800 grade) and fastened to a petrographic glass microscope slide (27 mm X 46 mm) with epoxide resin and hardener. This hardened on a hot plate for 30 minutes. The slide was placed on the swingarm of a

Hillquist grinder equipped with a diamond impregnated brass cup wheel, and the thin section was ground until it was almost thin enough to transmit light as viewed under a compound microscope (X 30). The resulting thin section was fine polished (800-1200 carborundum polishing grit series) until translucent, making growth lines distinguishable. The thin section was placed under a compound microscope and a drop of alcohol added to improve resolution. Pigmented growth lines were counted along a transect running from the dorsal to the ventral surface, as close as possible to the anterior end (umbo) in order that the first growth line would be counted. Each growth line was interpreted as annual, as described by Lutz (1976). Age vs. shell length data were accumulated in this manner from approximately 460 mussels from the four sites.

In conjunction with internal ageing, mussels were placed into categories of growth line progression (Table 12), following the method of Jones, 1980. There are two types of repeating, internal growth structures (increments) present within the inner shell layer of *M. edulis*. According to the terminology of Jones there are growth bands (GI II) which, in the case of *M. edulis*, are the widest of the two types and are generally a uniform white or pale brown colour, and there are growth lines (GI I) which are generally narrower (except often at the posterior end of shell thin sections) and are dark brown in colour. To best represent the seasonal progression, GI II was subdivided into three categories, a, b and c, which represented the order of increasing thickness of the growth band. GI I was not divided into categories and represented the stage at which the growth line (GI I) was just visible. These categories were analyzed in order to document the seasonal progression of growth increment formation, to assess synchrony within the population for the deposition of the growth line and to determine the degree of correlation with the spawning cycle.

Seasonal, linear shell growth could only be assessed to a limited extent. Estimates were obtained by measuring the distance from the last, external, winter check-mark to the tip of the growing edge of individual shells for June 25 and August 7 samples. The reasons for investigating seasonal growth were, firstly, to see if there was linear shell growth between winter growth cessation (i.e. December/January) and the time of first sampling, near the end of June. Such growth is particularily interesting from the point of view of the north shore mussels, since surface water temperatures from January—April are in the −1 to 0 C range, and in the May/June period are in the range of 1-4 C. It has been suggested (Loosanoff, 1942) that linear shell growth in M. edulis is negligible at temperatures less than 5 C. Secondly, differences in linear shell growth rate between the two sides of the Strait, over the periods winter to late June and winter to early August, might be attributable to the earlier surface water warming on the south shore (12-14 C in late June) and thus a faster start on that season's growth. Seasonal growth was examined in the arbitrarily chosen size groups: 15—30 mm and 31-45 mm.

STATISTICAL ANALYSIS

Growth

von Bertalanffy growth curves were generated for shell length vs. age data for 11 groupings of mussels representing the different sites and levels for the June-August (intertidal) and November (subtidal) sampling periods. The curves were derived via a SAS (Statistical Analysis System; Helwig and Council, 1979) computer package program (Marquardt method) which provides asymptotic 95% confidence intervals for the von Bertalanffy parameter estimates (L_∞, K, t_0). It was originally intended to use mussels from just one month's collection for deriving growth curves; however, after plotting both June and August length vs. age data it was discovered that within-month variability was as great as that between sampling times. In other words, any increase in shell length of August mussels over June samples was masked by individual variability in growth rates within both August and June. For this reason, late June and early August data were combined to generate von Bertalanffy growth curves for intertidal mussels. November data alone were used in deriving growth curves for subtidal mussels at Pte. Amour, Blanc-Sablon, and Anchor Pt., as it was felt that the growing period between June and November was too great to justify pooling of both data sets. In generating the growth curves, four June data points were excluded from the age vs. length data for Black Duck Cove low intertidal M. edulis. The four excluded points lay well below (8–10 mm) the remaining data points for the corresponding year classes, perhaps due to a combination of slow growth and one month shorter growing time than for August mussels.

Plots of shell width vs. shell length and shell height vs. shell length were made for high and low intertidal populations of M. edulis collected in August from all four sites. Least squares regression lines were fitted to the data. Between-site morphometric comparisons were then made through analysis of covariance for mussel populations collected at the same tidal level.

Allometric growth curves were generated for meat dry-weight vs. shell length, and shell weight vs. shell length, following the method of Ricker (1975). The least squares regression technique was used. The equation of the allometric curve is $W=aL^b$, where W represents weight, and L, length. Regression lines were generated for log meat weight vs. log shell length and log shell weight vs. log shell length data using the MINITAB computer package (Ryan et al., 1981). The slope of the regression line is 'b' in the equation, and the anti-log of the y-intercept of the regression line is coefficient 'a'. Analysis of covariance (ANCOVA:SPSS computer package; Nie et. al., 1975) was performed on regression lines and used as a significance test for comparing M. edulis populations at the same tidal level over the same sampling periods. Prior to performing ANCOVA, slopes of regression lines to be compared were tested for homogeneity through multiple regression analysis (SPSS: Statistical Package for the Social Sciences).

Replicate samples collected from the same tidal zone were pooled in order to generate allometric growth curves. Meat dry weights and shell weights of these replicate samples were compared by ANCOVA to assess within-tidal level variance.

In addition, with one low intertidal sample collected in November at Blanc-Sablon, meat weights and shell weights of top and bottom layer mussels within an aggregation were compared through ANCOVA.

Fecundity, Meat Dry-Weight Biomass, and Reproductive Output

Fecundity is that amount of the body mass which is gametes (eggs or sperm) and was calculated indirectly from pre-spawning/post-spawning meat weight changes using allometric curve predicted values for meat weight (Griffiths,1977; Thompson,1979; Bayne and Worrall, 1980; Kautsky,1982b). Bayne et al.(1983) report that their indirect and direct estimation methods produced comparable results. Fecundity was expressed as a function of age, where length/age data was derived from von Bertalanffy growth curves. In *M. edulis*, the mantle (gonad) undergoes pronounced seasonal weight changes correlated with the reproductive cycle, while the weight of somatic tissues remains relatively constant. I assumed therefore that these weight changes reflect changes in the gamete content of the mantle. Percentage weight loss at spawning represented the ratio of fecundity to total shell-free body weight.

Sample meat dry-weight biomass was estimated from size frequency data integrated with allometric growth curve estimates of average meat weight for a given size class. Reproductive output was then calculated as that proportion of total biomass which is devoted to gamete production, in other words the ratio of sample gamete biomass to meat weight biomass.

RESULTS

Surface water temperature and salinity data on the two sides of the Strait of Belle Isle are shown in Fig. 2. Cumulative surface water day degrees for the two sides, in the vicinity of the sites used in this study, are shown in Table 1. Day degrees is defined as the product of mean monthly temperature and days, with 0 C taken as the zero reference point for biological growth (Boetius, 1962).

REPRODUCTIVE CYCLE

State of the Gonad

In late June 1981, the majority of mussels at all sites had mantles with abundant follicles that covered approximately 80-90% of the mantle surface (i.e. pre-spawning condition) (Fig. 3). Mantles in June were also the thickest of the three sampling periods. In the high and low intertidal zones at Pte. Amour, a large proportion of mussels possessed thick mantles. At Blanc-Sablon and Black Duck Cove there was a large proportion of mussels with thin mantles. Approximately 50% of the mussels encountered in the subtidal zone at Pte. Amour and Anchor Pt., also had thin mantles.

There was a marked difference in the state of the gonads of specimens collected during the first week of August 1981, consistent at all sites and both tidal levels. The majority of mussels were in the thin or very thin categories and appeared either partially spent (Black Duck Cove) or fully spent with either no follicles visible or remnants of follicles and genital ducts present. Approximately 5-25% of the mussels at both tidal levels had follicles which were numerous and full of morphologically ripe gametes.

In late November, the great majority (60-100%) of mussels collected at all sites and levels were fully spent (post-spawned) and possessed thin or very thin mantles, reflecting very little post-spawning buildup of reserve material. There were also a few mussels (approximately 15%) which had follicles full of ripe gametes, although such follicles were sparsely distributed throughout the mantle.

Subtidal samples were not collected in all three months; however, of the samples examined, the same pattern encountered in the high and low intertidal zones was reflected in the subtidal zone.

Settlement

Table 2 shows the size and abundance of Mytilus edulis settling during 1981. Mussels smaller than 1.5 mm were assumed to have settled between August and November. Mussels in the 2-5 mm range were found in abundance in June, August, and November (Fig. 4). Heaviest settlement occurred at Black Duck Cove, particularily in the low intertidal zone where mussels $<$ 1.5 mm in shell length were found in concentrations equivalent to 15,000.m^{-2}. Although at Pte. Amour and Blanc-Sablon there were few mussels settling in the high intertidal, significant numbers settled in the high intertidal at Black Duck Cove. In the shallow subtidal at Blanc-Sablon, mussels < 1 mm in shell length were numerous, whereas, in the shallow subtidal (3 m) at Pte. Amour, small mussels (< 5 mm) were rare. All small mussels were found on adult mussel beds and therefore represented the secondary or final settlement phase for *Mytilus edulis*.

Fecundity

High Intertidal

At all sites fecundity increased with age, although at Blanc-Sablon and Black Duck Cove this increase was very gradual (Fig. 5). At Pte. Amour, fecundity increased rapidly for mussels aged 2 to 6 years, gradually leveling off past this age.

There was a large range in fecundity for any given age amongst the four sites. For example, for 6 year olds, the range in gamete weight spawned was from 14 mg dry weight at Black Duck Cove to 93 mg dry weight at Pte. Amour. Pte. Amour mussels had the greatest fecundity at any given age, with a maximum gamete dry wt. of 115 mg at age 12 years. Anchor Pt., Blanc-Sablon, and Black Duck Cove mussels were, as a group, far below these fecundity values, with post-spawning meat weight loss at these three sites being about 35, 22, and 14 mg respectively, for six year olds.

Low Intertidal

Fecundity increased with age and was greatest at Pte. Amour. At Anchor Pt., and Black Duck Cove fecundity increased rapidly up to the age of 8 years. The same relationship existed at Blanc-Sablon for ages older than 6 years. As well, there was a large range in fecundity values for a given age, ranging from approximately 23 mg at Blanc-Sablon to 160 mg at Pte. Amour, for six year old mussels.

Although there was a large range in fecundity between sites, the trend nonetheless was for fecundity within a site to be highest in the low intertidal (Fig. 5).

Percentage Body Weight (Shell-Free) Loss at Spawning

High Intertidal

Percentage weight loss in mussels was greatest at Pte. Amour, followed by Blanc-Sablon and Black Duck Cove (Fig. 6). At these three sites, percentage weight loss decreased with age; however, at Anchor Pt., it was seen to increase. For 2 year olds, values ranged from 25% at Black Duck Cove to 75% at

Pte. Amour, and for 6 year olds, from 20% at Black Duck Cove to about 50% at Pte. Amour. With the exception of older Anchor Pt., mussels, percentage weight loss was much greater at Pte. Amour than at all the other sites, for all ages.

Low Intertidal

At Pte. Amour, for mussels < 8 years of age, percentage weight loss was greater in the high intertidal than in the low intertidal (Fig. 6), however, for Black Duck Cove mussels, percentage weight loss at spawning was greater in the low intertidal. In the low intertidal, in contrast with the high intertidal, percentage weight loss revealed a decreasing trend with age at Anchor Pt., and an increasing trend at Blanc-Sablon. For 2 year olds, values ranged from 40% at Black Duck Cove to 58% at Pte. Amour, and for 6 year olds from 18% at Blanc-Sablon to 43% at Pte. Amour.

Meat Dry-Weight Biomass and Reproductive Output (Table 3)

The major contribution to meat weight biomass (g/200 cm) was made by mussels in the larger size classes (> 20 mm), in spite of the fact that smaller mussels (< 10 mm) dominated numerically at some sites (Anchor Pt., and Black Duck Cove in the high intertidal,, and Pte. Amour and Black Duck Cove in the low intertidal zone) (Fig. 7).

Low Intertidal

Biomass varied from 5.6 g/200 cm^2 at Black Duck Cove to 20.2 g/200 cm^2 at Anchor Pt. (280-1010g/m^2). If the contribution to biomass made by gametes is considered, values at Anchor Pt., and Black Duck Cove were similar (33% and 35%, respectively); whereas, on the north shore of the Strait, reproductive output was 46% and 16% of biomass at Pte. Amour and Blanc-Sablon respectively. At Pte. Amour, for mussels 20 mm in shell length, reproductive output was about 60% of total biomass (shell-free weight) and at Anchor Pt., it was about 55%.

High Intertidal

Biomass was uniformly low in this zone (3.3, 4.7, and 3.1 g/200 cm^2 at Anchor Pt., Blanc-Sablon and Black Duck Cove respectively). Reproductive output, as a percentage of biomass, varied from 43% at Anchor Pt., to 20% at Blanc-Sablon and 19.5% at Black Duck Cove.

Although mean biomass was 11.6 g/200 cm^2 in the low intertidal, as opposed to 3.7 g/200 cm^2 in the high intertidal, analysis of variance revealed no significant difference between the two tidal levels ($F(1,5)=4.28$, $p>0.05$) and this was due to the variance within the low intertidal (s.d.=6.4). As well, there was no significant difference ($p>0.05$) in reproductive output between the two tidal levels.

SIZE FREQUENCY ANALYSIS (Fig. 4)

High Intertidal

At Pte. Amour in June, the modal size class was 15-20 mm, while in August and November, the mode was the 5-10 mm size class. In addition, the 20-25 mm size class was abundant in November.

At Blanc-Sablon in both June and August, the four size classes between 15 and 35 mm were evenly represented. In June, there were no mussels < 15 mm in shell length, while in August there were none < 10 mm. In November, the 5-10 mm size class was by far the dominant group (frequency of 80%). In addition, a small number of mussels in the 40-45 mm size class were collected, the largest mussels found in the high intertidal at any site.

At Anchor Pt., in June, all size classes from 3-35 mm were represented. The mode consisted of size classes in the 15-25 mm range. In August, two size classes, 5-10 mm and 10-15 mm, comprised the mode. A very small proportion of mussels were in the 2-3 mm range.

At Black Duck Cove in June, the mode was represented by the 5-10 mm size class. All size classes in the 2-30 mm range were present, although sizes > 20 mm were rare. In August, the mode was the 10-15 mm group. In November, the mode was the 5-10 mm size class. An unquantified, but substantial, number of mussels < 2 mm were present as well.

Low Intertidal

In June, at Pte. Amour, the mode was represented by the 5-10 mm size class. Mussels were found in the 2-45 mm size range. In August, the clear mode was again the 5-10 mm size class. Mussels sampled were all < 40 mm in shell length.

At Blanc-Sablon in June, the mode was the 25-30 mm size class. Mussels were present in the range 15-40 mm. In August, the mode was the 25-30 mm size class. Mussels were present from 15-45 mm shell length although sparsely at sizes > 35 mm. In November the modal size class was 10-15 mm. Specimens from < 1 mm to 35 mm shell length were present.

At Anchor Pt., in June, there was no distinct mode, and size classes from 2-20 mm were evenly represented. In August there was a bimodal distribution, with sizes ranging from 3-40 mm.

At Black Duck Cove in June, the two size classes, 5-10 mm and 10-15 mm, dominated. Sizes from 2 to 40 mm were represented, although sizes > 30 mm were rare. In August, there was a bimodal distribution, with sizes ranging from 10-30 mm in shell length. In November, the mode was the 0-5 mm size class with sizes > 25 mm being sparsely represented.

Analysis of variance performed on abundance data (June and August samples) revealed no significant difference between low and high intertidal samples ($F(1,13)=1.76$, $p>0.05$).

GROWTH

Linear Shell Growth

Growth of Juvenile Mussels (low intertidal, June collections)

The majority of small mussels at Pte. Amour had produced their first external check-mark at a shell length of 1.5 mm or less (Table 4). If we consider just those mussels in the well-defined first check-mark category (one year olds ?), we find that the mean distance to this check-mark was 1.21 ± 0.37 mm (n=18). Distances to the second check-mark were more variable. Mussels with only two well-defined check-marks (i.e. two year olds) displayed a range in distance up to this second check-mark of 2.1-7.1 mm (n=15). Black Duck Cove _M. edulis_ are similar (Table 5). Looking at only those mussels with a well-defined first check-mark, the mean distance up to this check-mark was 1.09±0.49 mm (n=28). For those mussels with only two well-defined check-marks, the range in length to the second mark was 2.2-6.2 mm (n=8). For mussels with three well-defined check-marks (i.e. three year olds), the range in length to the third check-mark was 4.2-7.0 mm (n=8).

Growth of Adult Mussels (Von Bertalanffy parameter values and coefficients of determination are shown in Table 6).

Between-Site Comparisons (Figs.8,9,10)

High Intertidal

From the ages three to five years, mussels at Pte. Amour (Fig. 8) were approximately 3-4 mm longer than mussels of corresponding age classes from Blanc-Sablon, and close to 6 mm longer than similar aged mussels from Black Duck Cove or Anchor Pt. Past the ages of 5 and 6 years, however, growth abruptly slows. Given the range in length within year classes (Table 7), the initial faster growth rate of Pte. Amour mussels is not as apparent. The same is true if one only considers the Blanc-Sablon, Black Duck Cove, and Anchor Pt., growth curves. In fact, there is only a 1-2 mm difference between Black Duck Cove and Anchor Pt., curves, suggesting no difference.

Low Intertidal

Pte. Amour mussels had greater growth rates than mussels at the other sites by roughly the same order of magnitude difference in length as in the high intertidal zone (Fig.9). Blanc-Sablon and Black Duck Cove mussels had similar growth rates. Again, considering the within-year class variability, it is difficult to justify a statement that growth rates of mussels at Pte. Amour are highest of the three sites. The unusual Anchor Pt., growth curve is to a certain extent an artifact of the lack of data for older age classes (> 6 years). Thus, the growth curve is linear rather than sigmoidal, indicating little decrease in growth rate over the first six years at this site. This resulted in a non-credible L_∞ parameter value (486 mm). Although Pte. Amour intertidal mussels appear to live to a greater age than mussels at the other three sites, mussels in the 10, 11, and 12 year old age classes were represented by single observations.

Subtidal

Growth rates between sites were very similar (Fig.10).

Overall, for the combined data, there does not appear to be a trend for growth rates to be higher on either side of the Strait of Belle Isle.

Between-Tidal Level Comparisons (Fig. 11)

Shell growth rates decreased according to tidal level (e.g. high intertidal<low intertidal). In the younger age groups (e.g. 4 years), there is at least a 4-5 mm difference in length at corresponding ages between high and low intertidal mussels. At Pte. Amour (Fig. 11a) and Anchor Pt. (Fig. 11c), there is close to a 10 mm difference in length at age between high and low intertidal mussels for the older age classes (i.e. > 5 yrs.).

A common feature at all four sites and at all tidal levels is the large variation in growth rates within year classes (Tables 7,8,9). The overall, average range in length for a given year class, within the 11 categories of site and tidal level, was 10.4±1.9 mm. Comparison of meat weights and shell weights of M. edulis collected from the top and bottom of mussel 'clumps' (Blanc-Sablon low intertidal, Nov. 21, 200 cm^2) revealed no significant differences with regard to homogeneity of regression slopes and comparison of adjusted means (ANCOVA:P > 0.05). These mussels were not aged, however, to determine if there were differences in linear shell growth rates.

Growth curves at all sites and tidal levels indicate slow growth throughout a potentially long life span.

Seasonal Growth

Results from June samples (Table 10) suggest little if any difference in growth increments between north and south shore adult mussel populations, or between high and low intertidal mussels. Mean growth increments for this period varied between 0.9 and 1.6 mm in high intertidal mussels, and between 0.9 and 1.2 mm in low intertidal mussels. Subtidal growth increment means in the 15-30 mm size class (approximately 2 mm) were only slightly greater than in the high and low intertidal zones.

High intertidal growth increment means up to early August showed a similar pattern between north and south shores (Table 11), with values ranging between 1.5 and 2.2 mm between sites on either shore. In the low intertidal zone, however, both south shore sites had greater mean growth increment values than the two north shore sites (3.1 mm and 3.8 mm vs. 2.1 mm and 2.9 mm respectively). However, for the 15-30 mm size groups, t-tests revealed no significant differences in growth increment means between the two shores ($P > 0.05$). Growth increment variance was relatively large, indicating large variation in the onset of seasonal linear shell growth, or large variation in growth rates at these sites.

Seasonal Progression of Shell, Internal Growth Increments (Table 12)

High Intertidal

In late June, shell thin sections from sites on both shores revealed that the majority of mussels were in growth increment stage (GI) IIc (Pte. Amour, 100%; Blanc-Sablon, 100%; Black Duck Cove, 73%). In other words, they possessed a fully developed growth band and no recently formed growth line. One mussel from Black Duck Cove had just deposited a growth line (GI I) while two other mussels (18%) were in stage IIb, as they possessed a growth band which was half the thickness of the previous years band. Thin sections from samples taken during the first week of August revealed a striking difference in the proportional representation of the two growth increment types. A large percentage of mussels from the four sites had either recently deposited the growth line (GI I, 16-63%), or had deposited it earlier and were just forming the growth band (GI IIa, 12-56%). The percentage of mussels which still possessed a fully formed growth band, but which had not deposited a growth line, was much lower than in June (11-26%, as opposed to 73-100%). There were also those mussels, as in June, which possessed a 'half- thickness' growth band (5-24%). The term 'half-thickness' does not necessarily imply 'half-formed' (i.e: that a full half increment is yet to be deposited before the growth line is laid down). In fact, thickness of growth bands varies annually, particularily in shallow water bivalves (Rhoads and Pannella, 1970), and increments decrease in thickness as the mussels enter into the 'plateau-phase' of linear shell growth. Therefore, some of these 'half-formed' increments may have been fully formed.

Low Intertidal

In June, the situation was similar to that in the high intertidal, with one exception (Blanc-Sablon). At Pte. Amour and Black Duck Cove, the majority of mussels (89% and 80% respectively) possessed a fully formed growth band (GI IIc), while the percentage of mussels which had recently deposited a growth line was low (3% and 15%, respectively). As well, at Pte. Amour, 5% of the mussels had just begun to form a growth band. At Pte. Amour and Black Duck Cove, the percentage of mussels which possessed a half-thickness growth band was low (3% and 5% respectively). At Blanc-Sablon, a greater percentage of mussels had a relatively recently deposited growth line (stage GI I and GI IIa ; 7% and 43% respectively) than at the other sites. In addition, 14% had a half-thickness band, while only 36% of the mussels possessed a fully-formed band. In August, the change in composition of mussels in the various growth stages at the four sites that was noted in the high intertidal zone was also evident from low intertidal thin shell sections. While the percentage of mussels with a fully-formed growth band (GI IIc) ranged from 17-47%, the percentage of mussels with growth lines deposited since late June ranged from 3%-23% for stage GI I, and from 40%-47% for stage GI IIa. As well, from 7%-34% of the mussels were found in stage GI IIb.

Subtidal

Shell thin sections were examined from the months of May, June and November, 1981. Only one sample, at Pte. Amour, was collected in May. In this sample, 77% of the mussels possessed a fully formed growth band. Only one mussel appeared to have a recently formed growth line. At Pte. Amour and Anchor Pt., in June, the greatest percentage of mussels were in the same stage as mussels in the high and low intertidal (GI IIc ; 96% and 88% respectively). A very low percentage (3% and 4%) appeared to have a newly formed growth line. No subtidal samples were collected in August; however, in late November the greatest percentage of mussels were once more in stage GI IIc (95% at Pte. Amour, 100% at Blanc-Sablon, and 88% at Anchor Pt.).

From the examination of 500 shell thin-sections, it became evident that intertidal mussels deposited more pronounced growth lines than subtidal mussels. An exception to this were the pronounced growth lines deposited by shallow subtidal mussels at the November Anchor Pt. site.

Shell Morphometrics (Fig. 12)

Significant differences were found amongst many of the sites (Tables 13-16), in-spite of the fact that even in the most extreme cases between-site differences in shell width or shell height for a given shell length were < 2 mm. All regression equations have high values of the coefficient of determination. Significant differences between sites is a result of the very low variability within sites, which indicates a high degree of constancy of shell form in the midst of large variation in individual shell growth rates.

Growth in Weight

Growth in Shell Weight

The allometric equation, $W=aL^b$, is generally accepted as the best equation to fit data describing shell or meat weight as a function of shell length, and metabolic rate functions as a function of size in general (Hum, 1976). To test the goodness-of-fit of this equation to the present data, residuals from the data used to derive the allometric curves were analyzed from log-log plots of meat weight vs. shell length, and shell weight vs. shell length, for the entire August 1981 data set (high and low intertidal mussels). Two of the sixteen cases showed a distinct curvilinear trend, while two others showed slightly abnormal trends (one of which may have been due to a small sample size of 31). The allometric equation fit the data well in 12 out of 16 cases.

ANCOVA was performed on weight vs. length data. Relationships resulting from the analysis are presented below, followed by a re-interpretation, with lengths standardized through age, derived from von Bertalanffy growth curves. ANCOVA was performed on weight vs. length data, rather than weight vs. age data, because of the smaller variation in the former.

High Intertidal (Figs. 13a,d,f)

No pattern was evident from examination of relationships between sites from all three months. In June, Pte. Amour, Blanc-Sablon and Anchor Pt., mussels had similar shell weights for a given length. The slope of the regression line representing Black Duck Cove mussels was heterogeneous ($P < 0.05$) compared with the other three regression slopes. In August, however, the relationship among sites had changed; although not evident from the graph, weights between sites are dissimilar (Table 17). In November, relationships among sites had changed once more. The regression line slope for Pte. Amour was heterogeneous in comparison with Blanc-Sablon and Black Duck Cove regression slopes (Table 18). Black Duck Cove mussels had significantly greater shell weights than mussels of similar length at Blanc-Sablon.

Low Intertidal (Figs. 13b,e,g)

In June, while all regression line slopes were homogeneous, comparison of adjusted means revealed only Pte. Amour and Black Duck Cove, and Anchor Pt., and Black Duck Cove shell weights to be similar. From August data, residuals analysis of log-log plots of shell weight on shell length revealed trends in Black Duck Cove and Blanc-Sablon regressions. In the case of Blanc-Sablon the trend is curvilinear, such that for the smaller and larger size classes, weights were over-estimated. Taking this into consideration, ANCOVA revealed all four allometric curves to be similar. In November, shell weights at Black Duck Cove and Blanc-Sablon were not significantly different ($P>0.05$).

Subtidal (Figs. 13c,h)

Constantly submerged mussels displayed differences in shell weight between sites. Multiple regression analysis on June data from the two representative shore sites revealed heterogeneous slopes ($P < 0.05$). In the month of November, the regression line slope of Pte. Amour mussels was heterogeneous in comparison with the regression slopes of Blanc-Sablon and Anchor Pt. (Table 19). Regression lines for Blanc-Sablon and Anchor Pt. data had homogeneous slope values; however, subsequent ANCOVA revealed Blanc-Sablon mussels to have significantly greater shell weights than

Anchor Pt. mussels.

Shell Weight as a Function of Age and Tidal Level

When shell weight is expressed as a function of age (Fig. 14), trends can be seen which are not discernable in weight vs. length allometric curves. In the high intertidal, three out of four growth curves begin to approach an asymptote between the ages of five and six years; whereas, in the low intertidal and subtidal, none of the curves show any significant diminution in growth even at ages of eight and nine years. Shell weight as a function of shell length often reveals very similar weights between high and low intertidal mussels (Figs. 15a,c), however, if shell weight is considered as a function of age, low intertidal mussels have greater weights than high intertidal mussels of similar age (Figs. 15b and 15d).

Seasonal Shell Weight Changes

There was no seasonal pattern with respect to changes in shell weight between June and November, in both the high and low intertidal zones (Fig. 16). Compared to seasonal changes in meat weight, seasonal changes in shell weight are relatively minor (e.g. Black Duck Cove, low intertidal zone, Fig.16d).

Analysis of Replicate Samples

To determine how variable shell weight was within a tidal level, four sets of replicate samples (two high intertidal, two low intertidal pairs) were compared through ANCOVA. Of these, one low intertidal sample differed significantly from its replicate (heterogeneous slopes, $P < 0.05$).

Growth in Shell-Free Body Weight

High Intertidal (Figs. 17a,d,f)

Pre-spawned meat weights at Anchor Pt., Blanc-Sablon and Black Duck Cove in June were very similar; however, Pte. Amour weights were significantly greater (ANCOVA:$P < 0.05$) than weights at the other sites. In early August, meat weights had dropped greatly as mussels were now in the post-spawned condition. Pte. Amour, Blanc-Sablon and Black Duck Cove mussels all had similar meat weights and had significantly greater weights than mussels at Anchor Pt. (Table 20). In November, Pte. Amour mussels had greater meat weights than Black Duck Cove and Blanc-Sablon mussels. Black Duck Cove and Blanc-Sablon mussels had significantly different meat weights ($P<0.05$).

Low Intertidal (Figs. 17b,e,g)

In June, meat weights of mussels at Pte. Amour were significantly greater than meat weights at Blanc-Sablon, Black Duck Cove and Anchor Pt.. In contrast with the situation in the high intertidal, mussels at the other three sites did not have similar weights at this level. Anchor Pt. mussels had significantly greater weights than Black Duck Cove and Blanc-Sablon mussels at a given shell length, and Black Duck Cove mussels had greater meat weights than mussels at Blanc-Sablon (Table 21). In August, the slope of the Blanc-Sablon regression line was heterogeneous in comparison with Black Duck Cove and Anchor Pt., regression slopes. Black Duck Cove mussels had significantly lower weights than Pte. Amour mussels. Comparison of regression lines for Black Duck Cove and Blanc-Sablon November data revealed heterogeneous slopes ($P < 0.05$).

Subtidal (Figs. 17c,h)

In June, meat weights of mussels at Pte. Amour and Anchor Pt., were similar. However, whereas Pte. Amour and Blanc-Sablon mussels had almost identical meat weights in November, Anchor Pt., mussels had now dropped in weight significantly below mussels at the two former sites (Table 22).

Meat Weight as a Function of Age and Tidal Level

If shell lengths are replaced with von Bertalanffy-derived values of age at length (Fig. 18), it is seen that, as with shell weight, mussels in the high intertidal reach a lower weight asymptote at an earlier age, than do low intertidal mussels. Mussels collected from Pte. Amour and Anchor Pt., in June indicate that meat weight as a function of shell length was similar between tidal levels (Figs. 19a,c), however, meat weights of mussels older than two years of age are greater in the low intertidal than in the high intertidal (Figs. 19b,d).

Seasonal Changes in Meat Weight

In the high intertidal, from late June to early August, a large drop in meat weight occurred at all sites, although the extent of reduction in weight varied between sites. The greatest reduction occurred at Pte. Amour (Fig. 20a). Between June and August there was a drop in weight from 135 mg to 65 mg for a 25 mm mussel. By Nov.21, meat weight had risen to approximately 90 mg. At Blanc-Sablon (Fig. 20b), there was a smaller weight change between June and August, from approximately 95 mg to 75 mg, with weights of 50 mg by Nov.21. Black Duck Cove and Anchor Pt., mussels showed weight changes from approximately 90 mg in June to 75 mg and 50 mg in August respectively.

As in the high intertidal, mussels in the low intertidal at all sites displayed a drop in meat weight between June and August. Pte. Amour mussels showed the largest weight change (from 135 mg to 70 mg for a 25 mm mussel) (Fig.20c). Blanc-Sablon mussels showed only a slight change in weight (< 10 mg) at sizes < 30 mm. This weight change increased with the larger sizes but did not approach that occurring at Pte. Amour. At the two sites sampled in November (Black Duck Cove and Anchor Pt.), recovery in meat weight was barely above August values.

Unfortunately, no subtidal sampling was possible in August 1981; however, in June, 25 mm mussels at Pte. Amour and Anchor Pt., averaged 100 mg in dry meat weight, whereas at the end of November mussels averaged 80 mg and 50 mg meat weight at these respective sites (Figs. 17c,h).

Analysis of Replicate Samples

As with shell weight, replicate sample pairs were compared through ANCOVA to determine variability in meat weight within a tidal level. Of three sets of samples compared to their corresponding replicates, one pair differed significantly ($P < 0.05$).

DISCUSSION

REPRODUCTIVE CYCLE

Spawning

Mytilus edulis completes its full life-history within the Strait of Belle Isle in spite of the harsh physical conditions which these mussels, particularily the intertidal specimens, must endure. From observations on changes in the state of the gonad and seasonal changes in meat weight, it is apparent that spawning in M. edulis on both sides of the Strait of Belle Isle coincides with rising sea-water temperatures just as it does in other localities (Chipperfield, 1953; Wilson and Seed, 1974; Seed and Brown, 1977; Jorgensen, 1981; Kautsky, 1982b, Myint and Tyler, 1982). In the Strait, spawning appears to coincide with a rise in sea-water temperature into the 6-10 C range, although Newell et al. (1982) observed variation in timing between populations. Therefore, although the overall life-cycle is the same as in southern populations, the timing differs in Strait of Belle Isle mussels. This latitudinal affect on reproductive pattern is well-known and Seed (1976) calls attention to the extensive literature which suggests that mussels from more southerly waters spawn prior to those from colder, northern waters. However, Newell et al.(1982) found no latitudinal trend with regard to timing of the reproductive cycle in several populations along the United States eastern seaboard, and concluded that there was a temperature/food abundance relationship determining reproductive timing. Bayne and Worrall (1980), studying two adjacent mussel populations near Plymouth, England, found that spawning occurred in the summer at one site, but in the fall (September/October) at the other.

While a synchronized reproductive cycle is evident in Strait of Belle Isle <u>M. edulis</u>, the exact timing of peak spawning could not be determined, however within the July/early August period it was probably short and intense as is characteristic of marine invertebrates spawning in north temperate/subarctic regions (Thorson, 1950). Jorgensen (1981) claimed that a severe winter will tend to synchronize spawning the subsequent spring. Kautsky (1982b) stated that the large annual variations in temperature and food abundance in the Baltic Sea, give rise to a very marked pattern in reproductive activity. The relatively constant and severe nature of winters in the Strait of Belle Isle may result in reasonably predictable annual spawning cycles as well. Intensity of spawning may vary however, and local factors can result in variation in timing of spawning of populations in any given region. This has been observed, for instance, in Newfoundland (personal observation), New England (Newell et al., 1982), and Alimotos Bay (Moore and Reish, 1969) <u>M. edulis</u> populations. The majority of north temperate mussel populations appear to have a single peak spawning period per year, although certain populations from southwestern Britain and Northern Ireland are known to have two spawning periods per year (Wilson and Seed, 1974).

Bayne (1965) was able to maintain M. edulis in a suspended state of gametogenesis indefinitely at a temperature of 5 C. Since surface water temperatures on the north shore of the Strait of Belle Isle are in the 4-5 C range throughout June and only rise consistently above 5 C in July, maturation of gametes in mussels on the North Shore (e.g. Pte. Amour) of the Strait might be a rapid and very temperature dependent phenomenon. Myint and Tyler (1982) discovered that M. edulis could continue gametogenesis at very low temperatures (< 0 C); however, vitellogenesis (maturation) was suppressed. Although no evident differences in spawning time could be detected between the two sides of the Strait, histological examination of gonads, combined with more quantitative sampling, may reveal differences. Myint and Tyler (1982) believe that oocyte size and density provide the most information with regard to mussels experiencing different thermal stresses.

After spawning, mantles of mussels at all four sites were empty and transparent, as is found in other Newfoundland mussels following spawning (Hum, 1976; Thompson, 1979; personal observation), however, assuming no repeat spawning, mantles remained in this state to the end of November with little buildup of nutrient storage material (glycogen) which is part of the annual reproductive cycle in M. edulis (Gabbott, 1976; Bayne et al., 1982; Lowe et al., 1982). Earlier-spawning, southern mussel populations show [illegible] nutrient storage buildup (e.g. Ineze et al., 1980). This may indicate the extreme importance of the short period each year during which the spring phytoplankton bloom and rising water temperatures in the Strait of Belle Isle allow for the completion of gametogenesis. Freeman and Dickie (1979) observed, in Nova Scotian area mussels, that growth underwent a seasonal upsurge at the time of the spring phytoplankton bloom, their so-called, "cold-season growth". Kautsky (1982b) found that for all subtidal depths, the very swift increase in meat weight and gonadal development of Baltic mussels, could be directly correlated with the spring phytoplankton bloom. As in the Strait of Belle Isle, water temperatures in the Baltic during this period are generally < 5 C, and Kautsky (1982b) believes this indicates that food abundance is the primary factor controlling gonad growth in these mussels. Griffiths (1977) arrived at the same conclusion working with Choromytilus meridionalis and Aulacomya ater in south Africa.

Due to their small size, it was difficult to age mussels to their first year and determine whether or not they were mature. Mytilus edulis has the capability to breed in the first year of life (Seed,1969a; Seed and Brown, 1977). A comparison of Seed's stunted, exposed coast mussels with the small, exposed coast mussels of the Strait is useful, although Seed's population consists of a higher proportion of smaller individuals (< 5 mm). He observed that in areas of rapid (relative) growth maturity in the first year occurred at a shell length of 6-7 mm, whereas in areas of slow growth, mature individuals 2 mm in shell length could be found. He therefore concluded that for M. edulis, sexual maturity is a function of age, not size. On the Washington coast, Suchanek (1981) observed gonadal development in *M. edulis* at approximately 15-20 mm shell length, approximately 1-2 months after settlement, suggesting that depending upon locality, growth rates may determine whether or not maturation is more dependant upon size or age.

An age-specific, not size-specific, maturation appears to hold true for Strait of Belle Isle *Littorina saxatilis*, as male and female snails become mature at 4-5 mm shell height (unpublished data), which is in general a smaller size at maturity than in southern populations, and such a relationship may hold true for *M. edulis* as well.

Settlement

The large number of mussels < 2 mm in shell length collected in late November from both sides of the Strait of Belle Isle, may be indicative of a very late settlement period. Alternatively, there may be a relatively normal settlement period with regard to other Newfoundland mussels (July-September) combined with slow growth, or a combination of these two possibilities. The duration of the larval phase is quite variable, ranging from 3-10 weeks; however, in British waters and surrounding regions it is usually on the order of 3-4 weeks (Seed, 1969a). Kautsky (1981b) postulated a larval stage (pre-settlement) of 5-6 weeks duration for Baltic mussels, and he does not mention primary settlement.

Final size at settlement is variable and metamorphosis can be delayed for weeks if a suitable substratum is not found (Bayne, 1965). Individual mussels from a primary settlement on *Polysiphonia* in late September 1982 at Portugal Cove, Newfoundland, ranged in length from 300-800 microns (personal observation). *M. edulis* found in winter 1981 inside split *Ascophyllum nodosum* gas bladders at St. Phillips, Newfoundland, ranged from 600-3000 um in shell length (personal observation). Some of the larger mussels could have been storm washed immigrants, however, or even tide-dislodged, actively moving mussels, 3-4 mm in length (Nelson, 1928b). Thus, as in the plankton, residence times on algae varies depending upon time of settlement (summer or winter), along with other local factors. Differences in growth rates could also contribute to size variation. From the algae, early plantigrades migrate onto adult beds and are known as late plantigrades, from which they assume the adult habit.

Bayne (1964) points out that there is little information regarding the growth of late plantigrades immediately following settlement (< 2 mm). Given that peak summer surface water temperatures are relatively low in the Strait (ca. 8-10 C on the north side and 14-16 C on the south side), a maximum larval, planktonic phase lasting 1-2 months might be expected. However, because of the high mean flow rates (approximately 1 m/sec), a parcel of water could travel the length of the Strait in two days (Juszko, 1981). This leads to speculation on the location of parental stocks of larvae settling within the Strait. Taking into account a primary settlement phase on algae in the Strait (personal observation), the spawning period suggests that final settlement upon adult beds occurred sometime in September/October, with subsequent slow growth. Cold water temperatures (< 10 C) have been acknowledged as seriously curtailing metabolism and growth in larval and adult M. edulis (Nelson, 1928a; Bayne, 1965; Brenko and Calabrese, 1969; Myint and Tyler, 1982). In October and November, surface water temperatures on the north side of the Strait fall below 6 C, to 2 C in late November and similarily on the south side from approximately 10 C at the beginning of October to 2 C in late November. Low temperatures, in combination with significant wave exposure results in poor growing conditions for newly settled mussels.

Although mussels 1-2 mm in shell length were most abundant in late November, there was significant representation in the 2-5 mm range. These may have been mussels from the previous year which had over-wintered, at a small size, on algae. In fact, algal samples from the low intertidal zone at Blanc-Sablon in late June 1981 included associated mussels in the 1-2 mm size range. Larger mussels (e.g. 5 mm) found in late November could also have been the result of early spawning. Although there is a peak spawning nucleus each year within most mussel populations, there can be both early and late spawners. Seed (1969b) and Kautsky (1982b) point out how small mussels (2-5 mm), persistent throughout the year in dense populations and/or taken from exposed coast populations, can be incorrectly described as recently-settled, when in fact they may be stunted, competitively suppressed, older mussels. Judging from the size of mussels from the 1981 cohort in late November and from over-wintering sizes of previous year classes (interpreted from external, winter shell check-marks), the first-year classes of Strait of Belle Isle populations may largely over-winter at sizes < 2 mm. This phenomenon may affect whether or not mussels in this region start to spawn in their first year. Hum (1976) reports a late settlement of M. edulis at Holyrood, Newfoundland in which overwintering occurred at sizes of 1 mm. Dare and Davies (1975) observed that large intertidal settlements of "ground spat" (1-1.5 mm) in Wales remained in this size range for up to four months after the main winter/spring (December-April) settlement period.

Within the Strait of Belle Isle, settlement appeared heaviest at or just above low water level. Settlement was light in the high intertidal except at Black Duck Cove. The preference shown by mussel larvae to settle at or adjacent to low water level has been observed by others (i.e. Engle and Loosanoff, 1944) and is supported by the existence on most rocky shores of adult mussel beds at these tidal elevations. In the shallow subtidal (approximately 3 m below MLW) at Blanc-Sablon, spat settlement was also abundant and corroborates the findings of Engle and Loosanoff (1944), who found that at depths of 1 m below MLW the number of settled mussels approached that observed at MLW. Sutterlin et al. (1981) observed heavy mussel set at Avondale, Newfoundland, at depths < 3 m, although in general, spat settlement decreased with depth.

Fecundity, Biomass and Reproductive Output

The trend of increasing fecundity with size or age has been observed in numerous other studies (e.g. in bivalves: Griffiths, 1977; Thompson, 1979; Vahl, 1981; Kautsky, 1982b; and in species of Littorina: Hughes and Roberts, 1980). Fecundity was similar between sides of the Strait of Belle Isle. The large variation in fecundity between the four sites is not surprising considering that others (e.g. Thompson, 1979; Bayne and Worrall, 1980; Bayne et al., 1983) have found fecundity to vary annually and from population to population in relation to food availability. Furthermore, there may be variation due to differences in peak spawning periods, or completeness of spawning, between populations. Bayne and Worrall (1980) and Bayne and Widdows (1978) observed a reduction in fecundity in mussels exposed to temperature and nutritive stress. Temperature differences coupled with differences in ration, had a major effect on the fecundity of the mussels. In my study, individual gamete biomass, as a percentage of total biomass, ranged from 5-69% depending upon the site and individual size. Most values were in the 20-60% range indicating that gamete biomass can account for a significant proportion of total shell-free body weight which is in agreement with other studies in the literature (e.g. Griffiths, 1977; Thompson, 1979; Kautsky, 1981b).

Within the Strait, trends in fecundity, as a function of tidal level, are predictable and explainable, largely on the basis of longer feeding times and thus faster growth and greater production in the low intertidal as opposed to the high intertidal. More difficult to explain are differences observed between sites on the same shore and affinities found between opposite shore sites. Because food abundance (phytoplankton) was not considered here, it is not possible to discuss the role of this parameter in growth differences within the Strait of Belle Isle. The outstanding feature of the four sites is the high fecundity of Pte. Amour mussels in comparison with mussels from the other sites. Such differences are due, in part, to the relatively high growth rate of mussels at Pte. Amour in both the high and low intertidal zones.

Although there was no difference in meat dry weight biomass between high and low intertidal levels in this study, it is noted that this is a reflection of the sample size employed ($0.02\ m^2$) and due to the relative sparseness of mussels in the high intertidal zone, larger sample areas (e.g $1\ m$) would yield quite different results. Results, however, support the observation that meat weight as a function of shell length was similar between tidal levels (p.40). As a means of comparing reproductive patterns between different populations, reproductive output is not of much value without a knowledge of the size structure of the populations, since fecundity/somatic tissue weight relationships are correlated with size. As noted by Kautsky (1982b), and seen in this study, the contribution to biomass and reproductive output is very low for mussels < 15 mm in shell length despite their overall numerical dominance. One difference between Kautsky's findings and my results is that reproductive output from the various size-classes in the Strait of Belle Isle is much lower than for Baltic mussels, where in many size classes reproductive output can be 80% of pre-spawning meat weight.

GROWTH

Linear Shell Growth

There appears to be no pattern to intertidal growth rates between the two sides of the Strait of Belle Isle. Growth rates in the subtidal zone on both sides are similar in spite of a large difference in number of day-degrees. Mussels of the genus Mytilus combine tolerance to a wide range of environmental conditions with a flexibility of physiological response (Bayne and Worrall, 1980). M. edulis may compensate metabolically over the 6-8 C temperature difference between north and south sides of the Strait.

In comparing growth of M. edulis between populations, or between studies, one encounters the inherent difficulty of comparing results with respect to food abundance and tidal exposure. In terms of tidal exposure periods, M. edulis within the low intertidal or subtidal zones are reasonably comparable between sites; however, exposure times of high intertidal populations could vary from site to site. Baird (1966) and others have shown that as tidal level (= degree of tidal exposure) increases, growth rates of M. edulis rapidly decrease. Gillmor (1982) has shown that for M. edulis, the point of zero growth can be at an 80% exposure level (= tidal cycle emersion time). Characteristics of the shore locality (i.e. aerial climate), in combination with the physiological tolerances of the particular genetic stock, may determine the limit of upper extension of M. edulis. This suggestion has been made by others (e.g. Seed, 1969b).

Considering that growth in the intertidal consists of a tradeoff between energy input during submergence and energy cost during emersion, it is not surprising that absolute linear shell growth rates are greater in the low intertidal than in the high intertidal zone.

The variability seen in linear shell growth rates of mussels in the Strait of Belle Isle is a well-known characteristic of the species (e.g. Mossop, 1922; Lubinsky, 1958; Seed, 1969b; Stromgren, 1976; Riisgard and Randlov, 1981; Kautsky, 1982a), and also of C. virginica (e.g. Singh and Zouros, 1978; Koehn and Shumway, 1982; Singh, 1982). Reasons put forth to explain such variability include strong intraspecific competition (Kautsky, 1982a), intrinsic or genetic factors (Stromgren, 1976; Singh and Zouros, 1978; Newkirk, 1980; Jansen, 1982; Koehn and Shumway, 1982;), and density-dependent effects (Mossop, 1922; Wilson and Hodgkin, 1967; Seed, 1969b; Dare and Edwards, 1976; Broom, 1982).

Genetic differences in molluscs have been implicated in causing growth rate variation, and recent work with oysters (Koehn and Shumway, 1982) has revealed a possible biochemical/physiological involvement with regard to rate of oxygen metabolism. The literature recording both macro- and micro-geographic genetic variation within and between populations of mussels, other molluscs, and marine invertebrates in general, is extensive (e.g. Ahmed and Sparks, 1970; Koehn and Mitton, 1972; Milkman et al., 1972; Turano and Mitton, 1973; Levinton and Suchanek, 1978; Thorpe et al., 1978; Singh and Zouros, 1978; Gartner-Kepay et al., 1980; Haley and Newkirk, 1980; Black and Johnson, 1981; Bullhein and Scholl, 1981; Grove and Lester, 1982; Jansen, 1982)

In the Strait of Belle Isle, density effects on growth are probably maximal in the low intertidal and subtidal zones, and minimal in the high intertidal zone, where in most instances there was no clumping of mussels. Analysis of top and bottom layer M. edulis suggested that growth variability due to clumping was minimal at these sites; however, this suggestion is based solely on length/weight relationships and comparisons were not standardized through age. Freeman and Dickie (1979) and Harger (1967, cited in Harger 1972) are among the few others who have analyzed growth in M. edulis for density-dependent effects (i.e. separate vs. clumped), although others before have described " humping " or " clumping " phenomena in natural mussel populations (e.g. Mossop, 1922; Dare and Edwards, 1976). Harger (1967) found growth to be slower within clumps than on the outside of clumps. The Freeman and Dickie study showed little or no difference in linear shell growth rates in separated mussels vs. mussels within clumps. If density effects on growth are important, then depending upon the extent of compaction of the mussels, shell morphometric relationships will vary. The slight variation in shell form within Strait of Belle Isle <u>M. edulis</u> populations may indicate that density effects are minimal. It is not surprising that shell shape varies between sites, as shell morphometric relationships (e.g. height/length, width/length) are known to vary with environmental conditions (e.g. substrate, topography, wave exposure, population age composition, and density) (Lent, 1967; Seed, 1968).

There has apparently been a trend, at least in recent years, for mussels on both sides of the Strait of Belle Isle to over-winter at small sizes (e.g. < 2 mm). Over-wintering of mussels at small sizes has been observed in certain other arctic and north-temperate regions (e.g. Thule District, NW Greenland:Theisen, 1973; Southern Britain:Seed, 1969a,b; Wales:Dare and Davies, 1975; Baltic Sea:Kautsky, 1982a), and can be the result of a late settling period with little or no winter growth (Dare and Davies, 1975; this study). My study, and others (Seed, 1969b; Samtleben, 1977; Kautsky, 1982a) have also found that variation in growth rates of mussels < 10 mm in shell length can lead to a persistent population of small, stunted mussels (e.g. < 5 mm in length) which may be two or three years old, or older. This phenomenon is often found within dense, exposed coast populations (Seed, 1969b) or dense, brackish water populations (Kautsky, 1982a).

From the pronounced, external, winter check-marks on Strait of Belle Isle M. edulis it is also apparent that winter growth (Dec.-May?) is negligible; however, linear shell growth resumes while water temperatures are in the 0 - 5 C range. This study, and the work of others (Mossop,1922; Seed,1969b) has also revealed large variation in the start of seasonal growth within a population of mussels, possibly reflecting the proportion of "fast" and "slow" growers. Once again, the similarity in shell growth rates between sides of the Strait is apparent even during the spring/summer period when a surface water temperature difference is rapidly developing between the two shores.

If one compares linear shell growth rates of M. edulis from the literature, large differences in shell length for a given age are apparent. For example, the following shell lengths for 4 year old sublittoral mussels are available ; 100 mm (California:Harger 1970), 60 mm (Woods Hole: Hum 1976), 40 mm (Norway, Wallace 1980), 20 mm (Northern Greenland, Theisen, 1973), 30 mm (Holyrood, Newfoundland, Hum, 1976), and 35 mm (Pte. Amour, Labrador; this study). Such variation reflects differences in lengths of growing seasons amongst various geographical localities. There is a relatively predictable relationship between growth curve shape (i.e. von Bertalanffy curves) and latitudinal origin (Hum, 1976). Strait of Belle Isle M. edulis shell length/growth curves generally exhibit a gradual increase with a potential for a long life span. Hum (1976) found slow initial growth and a long life span in mussels at her northern stations. In contrast, growth at her southern stations was initially rapid but leveled off to a low value of L∞ in 1-2 yrs.

Seasonal Progression of the Annual Growth Line

There was a seasonal progression to the formation of the growth line which was relatively synchronous amongst populations at the four sites. This was true for both high and low intertidal specimens. Although there are insufficient data, there are indications that there is a similar trend among subtidal mussels as well. Mussels deposited almost a complete layer or band of nacre after the growth line was formed, before winter, which is similar to the findings of Lutz (1976). Although seasonal growth increment progression appears to be similar between sides of the Strait, more frequent sampling, combined with larger sample sizes, might reveal differences.

Shell Weight

As with shell morphometry, there are numerous factors causing variation in shell weight between or within tidal levels (degree of wave exposure, shell abrasion, and, possibly, spawning). Shell weight differences between populations at similar tidal levels are more difficult to explain.

Little seasonal variation in shell weight was apparent in my study, supporting Dare and Davies (1975) who stated that this was to be expected since the shell does not undergo an annual weight cycle. However, Cyr Couturier (personal communication), recorded a pronounced increase in shell weight for subtidal (2-3 m depth) M. edulis, during the spawning period at a time when shell length was relatively constant. Outside the spawning period, he observed that linear shell growth rate increased, and shell weight for a given shell length thus decreased. This would represent an annual shell weight cycle of the sort Dare and Davies (1975) suggested did not occur.

Soft Tissues

The soft tissues (gonadal) of north temperate mussels are known to undergo dramatic annual cycles of weight change which are directly related to the reproductive cycle (Dare and Edwards, 1975; Thompson, 1979; Bayne and Worrall, 1980; Kautsky, 1982b). While this cycle is distinguished by its pre-spawning weight buildup, a massive drop at spawning, and a gradual post-spawning weight increase, there are numerous variations which reflect differing reproductive patterns. The best examples of such exceptions are afforded by "trickle spawners" (e.g. Modiolus modiolus), or multiple spawners (e.g. Aulacomya ater), which display a fluctuating meat weight cycle throughout the year. Maximum meat weights in Western Atlantic M. edulis (Newfoundland region) occur prior to spawning (Thompson, 1979; Sutterlin et al., 1981; this study), and the post-spawning growing season is relatively short with consequently little build-up in meat weight prior to the next phytoplankton bloom the following spring. Exceptions to this apply to productive regions.

Comparing reported meat weights of mussels from various regions is made difficult by the problem of assessing "equal-opportunity environments" with regard to food availability. The relationships between phytoplankton abundance, feeding rates, and growth in Mytilids and other bivalves has been well studied (e.g. Thompson and Bayne, 1974; Paul et al., 1978; Widdows, 1978; Incze et al., 1980; Riisgard and Randlov, 1981; Navarro and Winter, 1982; Wright et al., 1982) and it has been shown that, in general, as phytoplankton concentrations increase so do growth rates. Although temperature and salinity are undoubtedly important factors with regard to growth rate, it appears that food abundance might be the single most important parameter controlling growth rates in bivalves. Kautsky (1982a) found a good correlation between growth rate and food abundance as did Winter (1978), Kiorboe et al. (1981), and Mohlenberg and Kiorboe (1981). Dare and Edwards (1976) found that a mid-summer fall in flesh content coincided with a sharp decline in phytoplankton concentrations in local inshore waters. Probably the most striking evidence in support of the supreme importance of food abundance with regard to growth rates comes from the work of Paul et al. (1978), in which M. edulis reared in a phytoplankton upwelling system grew to 30 mm in 90 days, whereas mussels from the fjord (at similar temperatures and salinities) required four years to reach this length. Future studies of Strait of Belle Isle M. edulis might focus on food abundance between the two shores and its effect upon growth.

Average meat weights in the Strait of Belle Isle are similar to those found in Baltic mussels by Kautsky (1982a) (e.g. 60 mg meat dry-weight for 30 mm mussels) although salinities are very different. In the Conway estuary, Dare and Edwards (1976) sampled 30 mm mussels weighing approximately 180 mg meat dry-weight and Bayne and Worrall (1980) report maximum meat weights of 200 mg for subtidal, 30 mm mussels at Belleyue, Newfoundland. Griffiths and King (1979) point out that food levels in the field vary unpredictably over a wide range, with the result that production rates may fluctuate greatly.

As predicted on the basis of available feeding time, age-specific meat weights of high intertidal mussels are less than those of low intertidal mussels.

GENERAL DISCUSSION

Predicted differences in growth rates between sides of the Strait of Belle Isle, on the basis of temperature differences, were not observed, and therefore metabolic compensation may be invoked to account for this. Fecundity, somatic tissue and shell growth were similar between the two sides of the Strait, although there were differences between the four sites that showed no pattern.

An alternative explanation is, because of low temperatures in the Strait of Belle Isle which are at the lower end of the range of temperatures experienced by Mytilus edulis throughout its geographical range, temperature differences result in an insignificant effect on growth rates. Coulthard (1929) reports growth in M. edulis between 3 and 25 C with optimum growth in the 10-20 C range. On the north side of the Strait of Belle Isle, monthly mean surface water temperatures are below 10 C whereas on the south shore, only four months have mean water temperatures greater than 10 C. Results of this study show that growth rates on both sides of the Strait of Belle Isle are slow. This is in agreement with the literature, which shows that growth rates of mussels from the Maritimes southward are relatively high (Mossop, 1922; Juszko, 1980), while being slower in more northern latitudes (Lubinsky, 1958; Theisen, 1973; Juszko, 1980).

Hum (1976) found large differences in growth rates between her sites over temperature differences of similar magnitude to those in the Strait of Belle Isle, however, temperatures at her sites were in a higher range than temperatures in the Strait of Belle Isle.

Despite the fact that mussels from both sides of the Strait displayed similar growth rates, food abundance in waters on both sides of the Strait remains to be assessed, in light of the strong influence which this variable exerts on fecundity (Bayne and Worrall, 1980), the overall course of the reproductive cycle (Kautsky, 1982b) and linear shell growth (Paul et al., 1978). Future work on M. edulis in the Strait of Belle Isle might include a determination of food abundance in surface waters between the two sides, relating this to observed growth rates.

Large year class variation in growth rates found in mussels on both sides of the Strait has been observed in other mussel populations as well (e.g. Mossop, 1922; Kautsky, 1982a). Although competition effects cannot be ruled out, the maintenance of heterogeneous genetic stocks through long distance larval dispersal is probably a key factor. Pertinent to this study would be an assessment of the extent of mixing of stocks between sides of the Strait of Belle Isle.

SUMMARY

Reproductive Cycle

1. Spawning appeared to be synchronized within and between sites over the sampling periods, in this study.
2. Fecundity in *Mytilus edulis* populations between the two sides of the Strait of Belle was similar, although between-site variation existed; fecundity was greater in the low intertidal than in the high intertidal, for for a given age.
3. Settlement in 1981 resulted in large numbers of mussels overwintering at shell lengths < 2 mm. Small mussels (e.g. 5 mm) were persistent in the population over the three sampling periods (June, August, November).

Growth

1. Growth rates (somatic tissue and shell) were similar between the two sides of the Strait of Belle Isle, although between-site differences existed.
2. Linear shell growth rates were low, typical of exposed coast populations. Low water temperatures in the Strait of Belle Isle, throughout much of the year, are implicated as well.
3. Despite large within-year-class variation in growth rates, shell morphometric relationships were constant

within sites, however, between-site differences existed.

4. The annual, spring start on linear shell growth varied within sites, and was similar between the two sides of the Strait.
5. The shell internal growth line was deposited at a time of rising water temperatures and spawning. The seasonal progression of the growth line was synchronous in populations between the two sides of the Strait.
6. Biomass values were low, typical of exposed coast populations which are dominated by small individuals.

Table 1. Annual cumulative surface water day degrees (D^o) (0^oC taken as zero reference point) for north and south shores of the Strait of Belle Isle, and other north temperate localities.

Locality	D^o	Reference
Cattewater (S. Britain)	5550	Bayne and Worrall (1980)
Menai Straits (N. Wales)	3600	Davies (1969)
Danish Wadden Sea	3318	Theisen (1968)
Thule (Greenland)	898	Theisen (1973)
Strait of Belle Isle (south shore)	2170	This study
Strait of Belle Isle (north shore)	950	This study

Table 2. Size and abundance of juvenile *Mytilus edulis* in the Strait of Belle Isle in November, 1981.

Site and level	Size class	Abundance (number per 200 cm^2)
Black Duck Cove low intertidal (Nov. 22)	≤1 mm	200
	>1-1.5 mm	100
	2-5 mm	50
Black Duck Cove high intertidal (Nov. 22)	≤1 mm	ca. 50
	>1-1.5 mm	ca. 50
Blanc-Sablon high intertidal (Nov. 22)	≤1 mm	1
Blanc-Sablon low intertidal (Nov. 20)	≤1 mm	14
	>1-1.5 mm	8
	3-5 mm	60
Blanc-Sablon subtidal (Nov. 21)	≤1 mm	ca. 50
	2-5 mm	<<50
Pte. Amour high intertidal (Nov. 21)	≤1 mm	0
	>1-1.5 mm	0
	2-5 mm	0
Pte. Amour subtidal (Nov. 21)	≤1 mm	0
	>1-1.5 mm	0
	2-5 mm	<<50

Table 3. Meat dry-weight biomass and reproductive output in Strait of Belle Isle *Mytilus edulis* populations.

Site	Tidal Level	Total Biomass ($g/_{200\ cm^2}$)	Total Biomass ($g/_{m^2}$)	Gamete Biomass ($g/_{200\ cm^2}$)	Gamete Biomass ($g/_{m^2}$)	$\frac{\text{Gamete Biomass}}{\text{Total Biomass}} \times 100$
PA	Low	12.7	635	5.9	295	46
BS	Low	8.0	400	1.2	61.5	16
BD	Low	5.6	280	1.9	98.5	35
AP	Low	20.2	1010	6.6	330	33
BS	High	4.7		0.9		20
AP	High	3.3		1.4		43
BD	High	3.1		0.6		20

Note: Since mussels did not cover an area of 1 m^2 anywhere in the high intertidal, biomass/$_{m}2$ was not calculated.

Table 4. External shell check marks on Pte. Amour low intertidal _Mytilus edulis_ collected June 21, 1981. (n=35)

(W=Well-Defined; D=Distinct)

Shell Length (mm)	Distance to Check mark (mm)		Shell Length (mm)	Distance to Check mark (mm)		
	1st	2nd		1st	2nd	3rd
2.7	0.8(W)	2.2(W)	7.0	1.3(W)	5.5(W)	6.8(D)
2.9	0.8(W)	2.1(W)	7.0	1.2(W)	5.0(W)	
3.0	1.0(D)	2.4(W)	7.2	1.2(W)	5.9(W)	
3.2	0.9(W)	2.4(W)	7.2	1.4(W)	3.0(D)	
3.3	1.1(D)	2.3(D)	7.3	1.9(W)	5.6(W)	
3.3	0.9(W)	2.4(W)	7.6	1.4(W)	6.2(W)	
3.3	0.4(D)	0.9(D)	7.8	1.5(W)	6.0(W)	
3.5	1.0(W)	3.0(W)	7.9	1.4(D)	6.0(W)	
3.6	0.9(W)	3.0(D)	8.2	1.8(D)	7.3(W)	
3.7	0.8(D)	2.8(W)	8.9	1.0(D)	6.7(D)	
3.7	0.4(D)	2.9(W)	9.0		6.6(W)	
3.8	1.1(D)	2.7(W)	9.0	2.0(W)	7.1(W)	
3.8	0.9(W)	2.6(W)	9.4	1.2(D)	7.0(W)	
4.3	1.1(D)	3.2(W)	9.6	1.4(D)	7.2(W)	
6.6	1.3(W)	4.9(D)	9.8	2.1(W)	7.0(W)	
6.7	0.8(W)	4.7(W)	11.7	1.2(D)	4.2(W)	10.1(W)
6.7	1.2(D)	5.3(W)				
6.8	1.8(D)	3.0(D)				
6.9	1.5(W)	6.0(W)				

Table 5 . External shell check marks on Black Duck Cove low intertidal *M. edulis* collected June 18, 1981 (n=63).
W = Well-Defined; D = Distinct

Shell Length (mm)	Distance to Check marks (mm)			Shell Length (mm)	Distance to Check marks (mm)				Shell Length (mm)	Distance to Check marks (mm)			
	1st	2nd	3rd		1st	2nd	3rd	4th		1st	2nd	3rd	4th
2.7	0.4(D)	1.8(W)		4.5	1.3(W)	3.6(D)			8.3	0.8(D)	3.7(D)	7.2(W)	
2.7	0.7(W)	2.0(D)		4.8	0.9(W)	-			8.3	0.9(D)	4.3(W)	7.3(D)	
2.8	0.6(D)	1.7(W)		5.3	0.9(W)	2.6(W)	4.2(W)		8.3	1.0(W)	3.9(W)	7.4(W)	
2.8	0.6(D)	2.1(W)		6.1	1.0(W)	3.0(W)	4.5(W)		8.5	0.6(D)	3.9(W)	7.0(D)	
2.9	1.1(W)	2.7(D)		6.2	0.7(D)	2.1(D)	5.0(W)		8.6	0.8(D)	3.3(D)	6.7(W)	
3.0	0.4(D)	1.6(D)		6.4	0.8(D)	3.7(W)	5.5(W)		8.6	0.8(W)	3.5(W)	7.0(W)	
3.1	1.0(W)	2.5(W)		6.4	0.8(D)	2.3(W)	5.9(D)		8.7	1.0(D)	3.9(D)	7.2(D)	
3.2	1.2(W)	2.3(W)		6.5	1.4(D)	4.9(D)			8.7	4.8(D)	7.8(D)		
3.2	0.8(W)	2.1(D)		6.6	0.9(D)	2.5(D)	4.7(W)		8.8	4.7(D)	6.4(W)	7.3(W)	
3.2	1.0(W)	2.2(W)		6.8	1.2(D)	3.0(D)	5.4(W)		9.0	0.8(D)	3.1(D)	7.5(W)	
3.3	1.3(D)	2.2(D)		7.0	0.8(W)	3.5(W)	5.6(W)		9.5	1.3(D)	5.1(W)	8.3(W)	
3.3	0.6(W)	2.5(D)		7.0	0.7(D)	2.7(D)	5.9(D)		12.6	1.0(W)	4.9(W)	10.4(D)	
3.3	1.0(W)	2.0(D)		7.1	0.8(D)	3.3(W)	5.7(W)		13.7	1.4(D)	6.0(W)	10.8(W)	12.4(W)
3.3	0.8(D)	2.2(W)		7.1	1.0(D)	4.0(W)	6.5(W)		13.7	1.1(D)	4.7(W)	8.2(D)	12.0(D)
3.4	0.8(D)	2.5(D)		7.1	1.0(D)	3.1(W)	5.6(D)						
3.4	0.4(D)	1.1(D)	2.5(W)	7.1	1.0(W)	3.1(W)	5.4(W)						
3.7	1.1(D)	2.0(W)		7.2	2.9(W)	5.7(W)							
3.8	1.1(W)	2.9(D)		7.3	2.0(D)	3.6(W)	6.3(D)						
3.9	0.8(D)	2.9(D)		7.3	1.0(W)	3.7(W)	5.5(W)						
4.1	1.0(D)	3.5(D)		7.4	0.8(D)	3.4(W)	5.0(D)	6.1(D)					
4.1	0.7(D)	1.9(W)	3.3(W)	7.5	2.4(W)	6.2(W)							
4.3	0.9(W)	1.7(D)	3.5(W)	7.7	1.4(W)	4.6(W)	6.8(W)						
4.4	0.8(W)	1.9(D)	3.5(D)	7.7	0.8(W)	4.0(W)	6.8(W)						
				7.8	1.4(W)								
				7.8	0.7(W)	2.3(W)							
				8.2	1.0(W)	4.7(W)							

Table 6. von Bertalanffy parameter values with 95% confidence limits and coefficients of determination for Strait of Belle Isle study sites. (L∞ - asymptotic length; K - intrinsic growth rate constant; t_o - time extrapolated to length = 0).

Site	Tidal Level	L∞ ± 95%	K ± 95%	t_o ± 95%	r^2
Pte. Amour	High	34.9 (24.8-45.0)	0.40 (-0.001-0.80)	1.21 (0.37-2.05)	0.65
	Low	44.7 (41.7-47.6)	0.37 (0.33-0.41)	1.19 (-0.07-2.45)	0.78
	Subtidal	53.4 (32.2-74.7)	0.23 (0.05-0.42)	0.19 (-0.81-0.42)	0.84
Blanc-Sablon	High	36.8 (20.1-53.4)	0.21 (-0.08-0.49)	0.05 (-2.35-2.45)	0.59
	Low	50.3 (-3.6-104.1)	0.17 (-0.17-0.50)	0.05 (-1.77-1.68)	0.69
	Subtidal	47.4 (31.3-63.4)	0.27 (0.07-0.48)	0.07 (-0.74-0.60)	0.78
Anchor Pt.	High	31.9 (-38.8-102.8)	0.23 (0.10-0.36)	0.06 (-0.73-0.85)	0.67
	Low	486.8 (152.95-162.68)	0.01 (-0.41-0.44)	0.09 (-3.77-3.58)	0.59
	Subtidal	48.1 (18.6-77.5)	0.33 (-0.19-0.85)	0.48 (-1.09-2.05)	0.62
Black Duck Cove	High	80.1 (-743-904)	0.05 (-0.59-0.68)	1.35 (-10.69-7.99)	0.46
	Low	62.7 (-68.8-194.2)	0.11 (-0.26-0.47)	0.55 (-4.13-3.03)	0.67

Table 7. Von Bertalanffy predicted shell length (mm) values with observed mean values and standard deviations for Strait of Belle Isle, high intertidal, *M. edulis* populations. Range (in parentheses) and number of specimens aged (n) indicated.

Age (Years)	Pte. Amour		Blanc-Sablon		Anchor Pt.		Black Duck Cove	
	Predict.	Observed	Predict.	Observed	Predict.	Observed.	Predict.	Observed
2	9.5	9.5±1.7(6.5-10.8) n=6	12.2	12.9 n=1	11.5	12.1±2.5(9.2-17) n=7	11.7	9.9±2.7(8-11.8) n=2
3	17.9	24.0 n=1	16.8	16.5±2.9(12.6-20.7) n=7	15.7	14.8±1.9(11.3-17.7) n=9	14.8	16.4±4.2(12-18) n=9
4	23.5	20.8±5.3(16.7-28.6) n=4	20.5	18.9±2.9(15.3-22.1) n=5	19.0	19.8±1.9(17.5-23) n=10	17.8	17.4±4.4(12.8-22.9) n=4
5	27.3	25.3±4.1(19.7-31.2) n=7	23.6	27.5±4.5(20.8-22.8) n=7	21.7	22.3±4.8(15.9-29.2) n=6	20.7	19.6±3.8(15.5-26.4) n=6
6	29.8	33.1±[illegible] (23.7-44.5) n=10	26.0	23.6±4.2(18-30.6) n=8	23.8	-	23.4	24.9±4(18.5-29.5) n=7
7	31.5	30.9±4.2(24.2-37.5) n=9	28.0	29.1 n=1	25.5	24.0 n=1	26.0	33.7±33(31.4-36) n=2
8	32.6	28.2±6.3(23.7-32.6) n=2	29.7	30.3±3.6(27.7-32.9) n=1				
9	33.4	-	31.0	28.2 n=1				
10	33.9	-	32.1	-				
11	34.2	32.6 n=1	32.9	35.7 n=1				
12	34.5	44.0 n=1						
Avg. Range in shell length (mm) per year class		11.8		9.1		8.3		6.0

Table 8. Von Bertalanffy predicted shell length [illegible] values with observed mean values and standard deviations for Strait of Belle Isle, low intertidal, *M. edulis* populations. Range (in parentheses) and number of specimens aged (n) indicated.

Age (Years)	Pte.Amour		Blanc-Sablon		Anchor Pt.		Black Duck Cove	
	Predict.	Observed	Predict.	Observed	Predict.	Observed	Predict.	Observed
1			8.1	9±2.3(7.4-10.6) n=2				
2	11.5	10.2±0.4(9.7-10.5) n=3	14.6	10.7±2.5(7.9-14.7) n=6	12.6	14.1±3.5(11.6-16.6) n=2	14.7	16.4±(14.2-18.6) n=3
3	21.6	22.8±4.6(13-29.6) n=13	20.1	19.8±3.6(15.6-24.4) n=6	18.5	17.5±4.2(13-26.4) n=12	19.5	18.7±3.7(12.7-23.1) n=12
4	28.7	28.4±5.0(18.3-35.8) n=13	24.7	24.8±6.2(17.5-36.3) n=7	25.2	25.1±5.3(16.4-34.1) n=11	23.8	24±3.6(19.6-29) n=6
5	33.6	37.2±1.9(24.2-38.9) n=5	28.6	30.5±4.7(26.2-37.4) n=6	30.0	28.7±7.2(17.6-36.8) n=7	27.7	27.6±4.1(22.5-35.7) n=6
6	37.0	35.2±4.5(26.7-41.6) n=13	32.0	31.1±6.6(21.6-41.2) n=12	35.7	36.1±3.3(33.3-40.3) n=4	31.2	33.1±5.2(24.7-38.6) n=5
7	39.3	31.5 n=1	34.8	31.2 n=1			34.3	32.1±5.5(28.8-38.5) n=3
8	41.0	42.7 n=1	37.2	34.4 n=1				
9	42.1	43.7±4.5(37-49.2) n=5						
10	42.9	44.8 n=1						
11	43.4	46.8 n=1						
12	43.8	42.6 n=1						
Avg.Range in shell length (mm) per year class		11.1		11.4		12.5		10.2

Table 9. Von Bertalanffy predicted shell length (mm) values with observed mean values and standard deviations for Strait of Belle Isle, subtidal, *M. edulis* populations. Range (in parentheses) and number of specimens aged (n) indicated.

Age	Pte. Amour		Blanc-Sablon		Anchor Pt.	
(Years)	Predict.	Observed	Predict.	Observed	Predict.	Observed
1	12.8	13.2±2.2(9.6-15.5) n=10	11.9	12.3±2.1(9.5-15.5) n=10		
2	21.2	19.6±2.4(16.1-22.8) n=5	20.4	19.2±3.1(15.1-21.7) n=4	18.9	19.6±1.4(17.8-21.2) n=5
3	27.9	28.6±8.1(20-37.8) n=16	26.9	26.6±6.1(18.9-37.7) n=13	27.1	26.1±3.6(18.2-31) n=14
4	33.2	31.8±4.3(25.2-37) n=5	31.8	36.2±6.3(29.5-42.1) n=3	33.0	34.7±6.7(22.2-44.3) n=9
5	37.3	38.1±6.1(28.6-46.5)	35.5	32.4±5.2(28.7-36) n=2	37.2	35.3±4.4(31.5-40.1) n=3
6	40.7	-	38.3	38.5 n=1	40.2	39.7 n=1
7	43.3	42.2 n=1	40.5	-		
8			42.1	-		
9			43.4	43.1 n=1		
Avg. Range in shell length (mm) per year class		10.2		12.0		11.7

Table 10. Growth in length of the shell (mm) from last winter growth-interruption mark to margin of growing edge.

Site	Date	Tidal Zone					
		High Intertidal		Low Intertidal		Subtidal	
		Size Class (mm)					
		15-30	31-45	15-30	31-45	15-30	31-45
Pte. Amour	June 21/81	1.4±0.8 (n=12)	1.6±1.1 (n=17)	1.2±0.6 (n=23)	0.9±0.6 (n=16)	2.1±0.8 (n=15)	-
Blanc-Sablon	June 21/81	0.9±0.9 (n=12)	-	-	-	-	-
Black Duck Cove	June 18/81	1.4±0.6 (n=12)	-	-	-	-	-
Anchor Pt.	June 18/81	-	-	-	-	2.0±0.8 (n=27)	1.2±0.7 (n=5)

Table 11. Growth in length of the shell (mm) from last winter growth-interruption mark to margin of growing edge.

Site	Date	Tidal Zone			
		High Intertidal		Low Intertidal	
		Size Class (mm)			
		15-30	31-45	15-30	31-45
Pte. Amour	Aug. 3/81	2.2±1.5 (n=23)	-	2.9±2.0 (n=14)	-
Blanc-Sablon	Aug. 4/81	1.6±1.1 (n=31)	-	2.1±0.9 (n=21)	1.9±1.2 (n=13)
Black Duck Cove	Aug. 5/81	2.1±0.8 (n=34)	-	3.8±1.9 (n=21)	-
Anchor Pt.	Aug. [illegible]/81	1.4±0.8 (n=38)	-	3.1±1.8 (n=17)	2.5±0.9 (n=4)

Table 12. Seasonal progression of growth increments in Strait of Belle Isle *M. edulis*.
(N=no data; PA=Pte.Amour; BS=Blanc-Sablon; AP=Anchor Pt.; BD=Black Duck Cove).

Growth Increment	Stage	Longitudinal Shell Section Showing Ventral Shell Margin	Description	High Intertidal								Low Intertidal								Subtidal					
				June				August				June				August				May	June		November			
				PA	BS	AP	BD	PA	BS	AP	BD	PA	BS	AP	BD	PA	BS	AP	BD	PA	PA	AP	PA	BS	AP	
GI I			GI I forming at edge	0	0	N	1 (9)	4 (22)	10 (63)	13 (35)	3 (16)	1 (3)	1 (7)	N	3 (15)	1 (6)	5 (23)	1 (3)	1 (7)	0	1 (4)	1 (3)	0	0	1 (3)	
GI II	IIa		GI formed, GI II begun	0	0	N	0	10 (56)	2 (12)	11 (30)	8 (42)	2 (5)	6 (43)	N	0	8 (47)	9 (41)	16 (46)	6 (40)	1 (8)	0	0	0	0	0	
	IIb		GI II [illegible] complete	0	0	N	2 (18)	1 (5)	0	9 (24)	3 (16)	1 (3)	2 (14)	N	1 (5)	0	2 (9)	12 (34)	1 (7)	2 (15)	0	3 (9)	1 (5)	0	3 (9)	
	IIc		GI II 3/4 to fully complete	19 (100)	14 (100)	N	8 (73)	3 (17)	4 (25)	4 (11)	5 (26)	33 (89)	5 (36)	N	16 (80)	8 (47)	6 (27)	6 (17)	7 (46)	10 (77)	25 (96)	30 (88)	20 (95)	17 (100)	30 (88)	No. %
Total Number of Shells				19	14	N	11	18	16	37	19	37	14	N	20	17	22	35	15	13	26	34	21	17	34	

Table 13. Ancova results. Shell width on shell length (log-log plots): high intertidal *M. edulis*.

Model to Test Homogeneity of Slopes (Significance Level = 0.05)

Ho	Source of Variation	DF	SS	MS	F	Signif. of F
Slopes of all regression lines are homogeneous (parallel or fall on same line)	Between Regressions	3	4.504	1.501	3.83	$p < 0.05$
	Within Regressions	189	74.165	0.392		
	Blanc-Sablon differs significantly from Anchor Pt.					$(p < 0.05)$
	Blanc-Sablon differs significantly from Black Duck C.					$(p < 0.05)$
	Pte.Amour differs significantly from Anchor Pt.					$(p < 0.001)$
	Anchor Pt. differs significantly from Black Duck C.					$(p < 0.001)$

Analysis of Covariance Performed on Regression with Homogeneous Slopes

Ho	Comparisons	Signif.
There is no difference between sites after the covariate length is adjusted for	Pte.Amour/Blanc-Sablon	ns
	Pte.Amour/Black Duck C.	ns

Table 14. Ancova results. Shell height on shell length (log-log plots); high intertidal *M. edulis*.

Model to Test Homogeneity of Slopes (Significance Level = 0.05)

Ho	Source of Variation	DF	SS	MS	F	Signif. of F
Slopes of all regression lines are homogeneous (parallel or fall on same line)	Between Regressions	3	3.042	1.014	4.875	$p < 0.005$
	Within Regressions	190	39.606	0.208		

Pte. Amour differs significantly from Anchor Pt. ($p < 0.05$)

Pte. Amour differs significantly from Black Duck C. ($p < 0.01$)

Analysis of Covariance Performed on Regressions with Homogeneous Slopes

Ho	Comparisons	Signif.
There is no difference between sites after the covariate length is adjusted for	Blanc-Sablon/Pte. Amour	ns
	Blanc-Sablon/Anchor Pt.	ns
	Blanc-Sablon/Black Duck C.	ns
	Anchor Pt./Black Duck C.	ns

Table 15. Ancova results. Shell width on shell length (log-log plots): low intertidal *M. edulis*.

Model to Test Homogeneity of Slopes (Significance Level = 0.05)

Ho	Source of Variation	DF	SS	MS	F	Signif. of F
Slopes of all regression lines are homogeneous (parallel or fall on same line)	Between Regressions	3	7.652	2.55	3.96	$p < 0.01$
	Within Regressions	157	100.9	0.643		

Blanc-Sablon differs significantly from Pte. Amour ($p < 0.001$)

Blanc-Sablon differs significantly from Black Duck C. ($p < 0.0001$)

Pte.Amour differs significantly from Anchor Pt. ($p < 0.01$)

Black Duck C. differs significantly from Anchor Pt. ($p < 0.01$)

Analysis of Covariance Performed on Regressions with Homogeneous Slopes

Ho	Comparisons	Signif.
There is no difference between sites after the co-variate length is adjusted for.	Blanc-Sablon/Anchor Pt.	$p < 0.05$
	Pte. Amour/Black Duck C.	ns

Table 16. Ancova results. Shell height on shell length (log-log plots): low intertidal *M. edulis*.

Model to Test Homogeneity of Slopes (Significance Level = 0.05)

Ho	Source of Variation	DF	SS	MS	F	Signif. of F
Slopes of all regression lines are homogeneous (parallel or fall on same line)	Between Regressions	3	8.629	2.876	3.528	$p < 0.05$
	Within Regressions	157	127.901	0.815		

Blanc-Sablon differs significantly from Anchor Pt. ($p < 0.05$)

Pte.Amour differs significantly from Anchor Pt. ($p < 0.05$)

Anchor Pt. differs significantly from Black Duck C. ($p < 0.05$)

Analysis of Covariance Performed on Regressions with Homogeneous Slopes

Ho	Comparisons	Signif.
There is no difference between sites after the co-variate length is adjusted for	Blanc-Sablon/Pte. Amour	ns
	Blanc-Sablon/Black Duck C.	ns
	Pte.Amour/Black Duck C.	ns

Table 17. Ancova results. Shell weight on shell length (log-log plots): high intertidal M. edulis collected in August.

Model to Test Homogeneity of Slopes (Significance Level = 0.05).

Ho	Source of Variation	DF	SS	MS	F	Signif. of F
Slopes of all regression lines are homogeneous (parallel or fall on same line)	Between Regressions	3	0.086	0.0287	3.588	$p < 0.05$
	Within Regressions	171	1.391	0.008		

Blanc-Sablon differs significantly from Anchor Pt. $F_{(1,106)}=5.82$ $(p<0.05)$

Blanc-Sablon differs significantly from Black Duck C. $F_{(1,92)}=7.79$ $(p<0.01)$

Analysis of Covariance Performed on Regressions with Homogeneous Slopes

Ho	Comparisons	F	Signif. of F
There is no difference between sites after the co-variate length is adjusted for	Blanc-Sablon/Pte.Amour	$F_{(1,78)}=9.199$	$p < 0.005$
	Anchor Pt./Black Duck C.	$F_{(1,95)}=21.05$	$p < 0.001$
	Pte.Amour/Black Duck C.	$F_{(1,66)}=6.375$	$p < 0.05$
	Pte.Amour/Anchor Pt.	$F_{(1,80)}=5.691$	$p < 0.05$

Table 18. Ancova results. Shell weight on shell length (log-log plots): high intertidal *M. edulis* collected in November.

Model to Test Homogeneity of Slopes (Significance Level = 0.05)

Ho	Source of Variation	DF	SS	MS	F	Signif. of F
Slopes of all regression lines are homogeneous (parallel or fall on same line)	Between Regressions	2	0.061	0.031	5.166	$p < 0.05$
	Within Regressions	117	0.717	0.006		

Pte.Amour differs significantly from Blanc-Sablon $F_{(1,65)}=8.88$ $(p<0.005)$

Pte.Amour differs significantly from Black Duck C. $F_{(1,87)}=4.37$ $(p<0.05)$

Analysis of Covariance Performed on Regressions with Homogeneous Slopes

Ho	Comparisons	F	Signif. of F
There is no difference between sites after the covariate length is adjusted for	Blanc-Sablon/Black Duck C.	$F_{(1,83)}=12.005$	$p < 0.005$

Table 19. Ancova results. Shell weight on shell length (log-log plots): subtidal *M. edulis* collected in November.

Model to Test Homogeneity of Slopes (Significance Level = 0.05)

Ho	Source of Variation	DF	SS	MS	F	Signif. of F
Slopes of all regression lines are homogeneous (parallel or fall on same line)	Between Regressions	2	0.215	0.108	12	$p < 0.001$
	Within Regressions	156	1.472	0.009		

Pte.Amour differs significantly from Anchor Pt. $F_{(1,102)}=19.52$ $(p<0.05)$

Pte.Amour differs significantly from Blanc-Sablon $F_{(1,107)}=7.75$ $(p<0.05)$

Analysis of Covariance Performed on Regressions with Homogeneous Slopes

Ho	Comparisons	F	Signif. of F
There is no difference between sites after the co-variate—length is adjusted for	Blanc-Sablon/Anchor Pt.	$F_{(1,104)}=13.051$	$p < 0.001$

Table 20. Ancova results.. Meat weight on shell length (log-log plots): high intertidal *M. edulis* collected in August.

Model to Test Homogeneity of Slopes (Significance Level = 0.05)

Ho	Source of Variation	DF	SS	MS	F	Signif. of F
Slopes of all regression lines are homogeneous (parallel or fall on the same line)	Between Regressions	3	0.101	0.034	1.03	ns
	Within Regressions	127	4.149	0.033		

Analysis of Covariance Performed on Regressions with Homogeneous Slopes

Ho	Comparisons	F	Signif. of F
There is no difference between sites after the covariate length is adjusted for	Pte. Amour/Black Duck C.	$F_{(1,54)}=0.365$	ns
	Blanc-Sablon/Black Duck C.	$F_{(1,62)}=2.572$	ns
	Blanc-Sablon/Anchor Pt.	$F_{(1,75)}=5.002$	$p < 0.05$
	Pte.Amour/Blanc-Sablon	$F_{(1,51)}=0.593$	ns
	Pte.Amour/Anchor Pt.	$F_{(1,67)}=8.518$	$p < 0.005$
	Anchor Pt./Black Duck C.	$F_{(1,78)}=11.864$	$p < 0.001$

Table 21. Ancova results. Meat weight on shell length (log-log plots): low intertidal *M. edulis* collected in June.

Model to Test Homogeneity of Slopes (Significance Level = 0.05)

Ho	Source of Variation	DF	SS	MS	F	Signif. of F
Slopes of all regression lines are homogeneous (parallel or fall on the same line)	Between Regressions	3	0.0557	0.0186	1.65	ns
	Within Regressions	209	2,358	0.0113		

Analysis of Covariance Performed on Regressions with Homogeneous Slopes

Ho	Comparisons	F	Signif. of F
There is no difference between sites after the covariate length is adjusted for	Pte. Amour/Black Duck C.	$F_{(1,101)}=51.398$	$p < 0.001$
	Blanc-Sablon/Black Duck C.	$F_{(1,116)}=83.774$	$p < 0.001$
	Blanc-Sablon/Anchor Pt.	$F_{(1,110)}=112.669$	$p < 0.001$
	Pte. Amour/Blanc-Sablon	$F_{(1,110)}=150.79$	$p < 0.001$
	Pte. Amour/Anchor Pt.	$F_{(1,97)}=4.764$	$p < 0.05$
	Anchor Pt./Black Duck C.	$F_{(1,101)}=38.638$	$p < 0.001$

Table 22. Ancova results. Meat weight on shell/length (log-log plots): subtidal *M. edulis* collected in November.

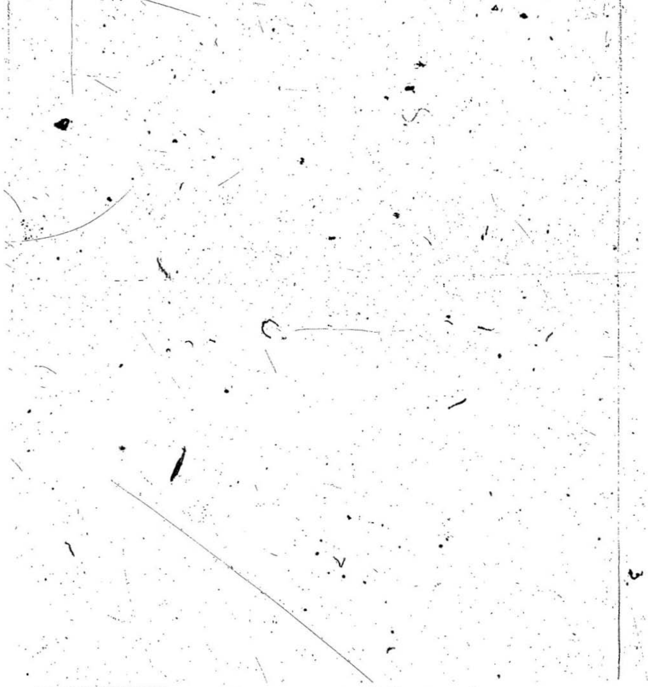
Model to Test Homogeneity of Slopes (Significance Level = 0.05)

Ho	Source of Variation	DF	SS	MS	F	Signif. of F
Slopes of all regression lines are homogeneous (parallel or fall on the same line)	Between Regressions	2	0.012	0.006	0.462	ns
	Within Regressions	155	2.048	0.013		

Analysis of Covariance Performed on Regressions with Homogeneous Slopes

Ho	Comparisons	F	Signif. of F
There is no difference between sites after the covariate length is adjusted for	Pte.Amour/Blanc-Sablon	$F_{(1,105)}=0.054$	ns
	Pte.Amour/Anchor Pt.	$F_{(1,102)}=115.165$	$p < 0.001$
	Blanc-Sablon/Anchor Pt.	$F_{(1,104)}=13.051$	$p < 0.001$

FIGURE 1. Map of Strait of Belle Isle study areas and surrounding regions.



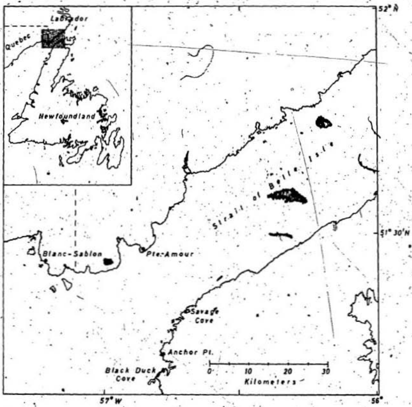

Labrador
Quebec
Newfoundland
52° N
Strait of Belle Isle
51° 30' N
Blanc-Sablon
Pte.-Amour
Savage Cove
Anchor Pt.
Black Duck Cove
0
10
20
30
Kilometers
57° W
56°

FIGURE 2. Surface water, temperature and salinity profiles for north and south shores of the Strait of Belle Isle.

TOP: Monthly average, surface water temperatures for north (thin line) and south (thick line) shore sites.

Inset- Thermograph data for Pte. Amour, mid-intertidal region.

BOTTOM: Temperature and salinity data at 11 m depth for Savage Cove and Pte. Amour.
Dashed line: salinity
Solid line: temperature
Thick line: Savage Cove
Thin line: Pte. Amour

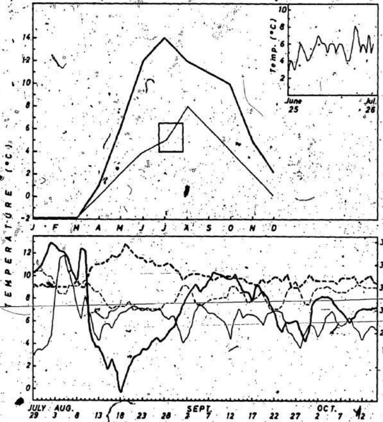

TEMPERATURE (°C)
14
12
10
8
6
4
2
0
-2
J F M A M J J A S O N D
Temp. (°C)
10
8
6
4
2
June 25
Jul. 26
12
10
8
6
4
2
0
33
32
31
30
29
SALINITY (PPT)
JULY 29
AUG. 3
8
13
18
23
28
SEPT. 2
7
12
17
22
27
OCT. 2
7
12

FIGURE 3. Percent frequency of <u>M. edulis</u> in various spawning stages at <u>Pte</u>. Amour, Blanc-Sablon, and Black Duck Cove in June, August and November, 1981.

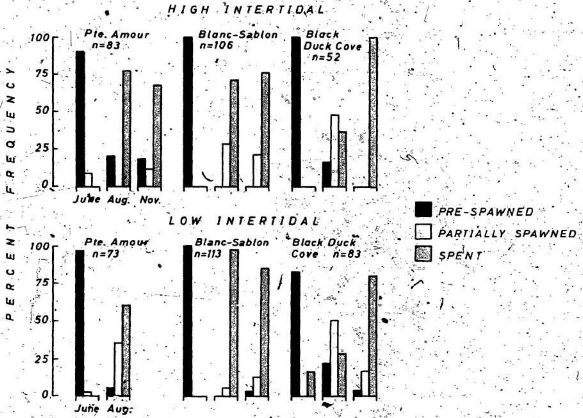

HIGH INTERTIDAL
LOW INTERTIDAL
PERCENT FREQUENCY
100
75
50
25
0
Pte. Amour n=83
Blanc-Sablon n=106
Black Duck Cove n=52
June
Aug.
Nov.
Pte. Amour n=73
Blanc-Sablon n=113
Black Duck Cove n=83
PRE-SPAWNED
PARTIALLY SPAWNED
SPENT

FIGURE 4. Shell length frequencies of Strait of Belle Isle intertidal *M. edulis* populations.
(PA:Pte. Amour; BS:Blanc-Sablon; AP:Anchor Pt.; BD:Black Duck Cove).
Hatching represents an unquantified number of mussels in the 2-5 mm range.

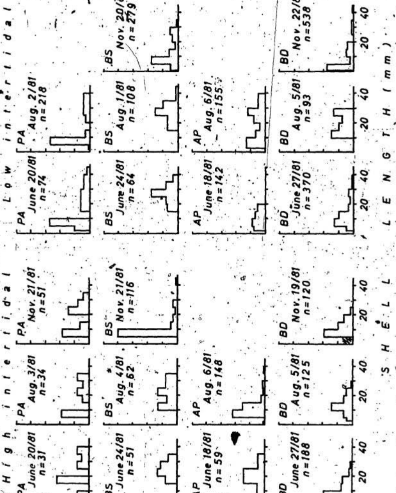

High intertidal
Low intertidal
PA June 20/81 n=31
PA Aug. 3/81 n=34
PA Nov. 21/81 n=51
PA June 20/81 n=74
PA Aug. 2/81 n=218
BS June 24/81 n=51
BS Aug. 4/81 n=62
BS Nov. 21/81 n=116
BS June 24/81 n=64
BS Aug. 1/81 n=108
BS Nov. 20/81 n=279
AP June 18/81 n=59
AP Aug. 6/81 n=148
AP June 18/81 n=142
AP Aug. 6/81 n=155
BD June 27/81 n=188
BD Aug. 5/81 n=125
BD Nov. 19/81 n=120
BD June 27/81 n=370
BD Aug. 5/81 n=93
BD Nov. 22/81 n=538
100
60
20
20
40
PERCENT FREQUENCY
SHELL LENGTH (mm)

FIGURE 5. Age-specific fecundity in Strait of Belle Isle *M. edulis* populations. (PA:Pte. Amour; BS:Blanc-Sablon; BD:Black Duck Cove; AP: Anchor Pt.).

solid line: high intertidal.
dashed line: low intertidal.

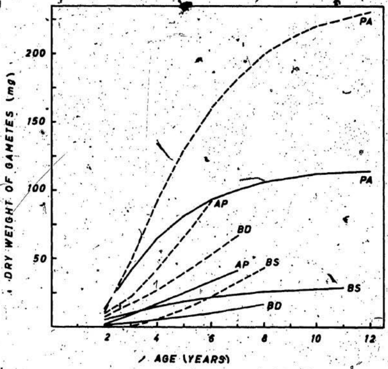

DRY WEIGHT OF GAMETES (mg)
200
150
100
50
2
4
6
8
10
12
AGE (YEARS)
PA
PA
AP
BD
AP
BS
BS
BD

FIGURE 6. Gamete weight as a percentage of total shell-free body weight in Strait of Belle Isle *M. edulis*.

solid line: high intertidal.
dashed line: low intertidal.

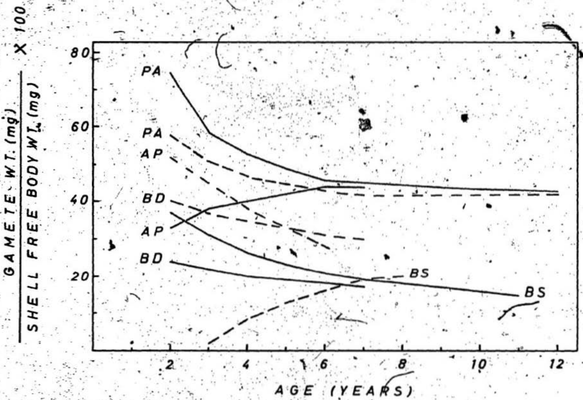

GAMETE WT. (mg) / SHELL FREE BODY WT. (mg) X 100
80
60
40
20
PA
PA
AP
BD
AP
BD
BS
BS
2
4
6
8
10
12
AGE (YEARS)

FIGURE 7. Meat dry-weight biomass, abundance, and reproductive output in Strait of Belle Isle intertidal *M. edulis* populations.

histograms: abundance.
line graph: total meat weight.
stipple: gamete weight.

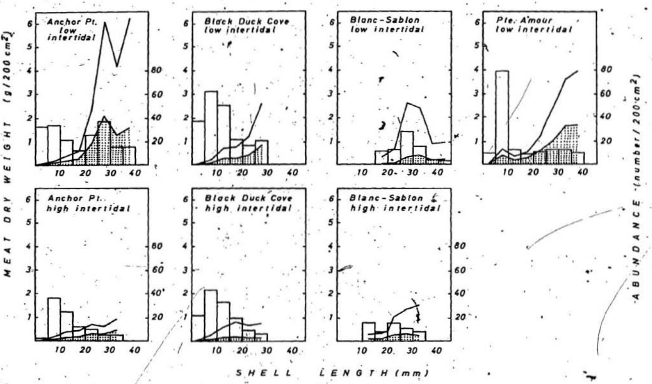

Anchor Pt. low intertidal
Black Duck Cove low intertidal
Blanc-Sablon low intertidal
Pte. Amour low intertidal
Anchor Pt. high intertidal
Black Duck Cove high intertidal
Blanc-Sablon high intertidal
MEAT DRY WEIGHT (g/200 cm²)
ABUNDANCE (number / 200 cm²)
SHELL LENGTH (mm)
1
2
3
4
5
6
20
40
60
80
10
20
30
40

FIGURE 8. von Bertalanffy linear shell growth curves for high intertidal Strait of Belle Isle *M. edulis* populations.

circles: mean lengths at north shore sites (Pte. Amour, Blanc-Sablon).
triangles: mean lengths at south shore sites (Anchor Pt., Black Duck Cove).
closed vertical bars: 95% confidence limits about means.
open vertical bars: ranges for n=2 observations.
points with no bars: n=1 observations.

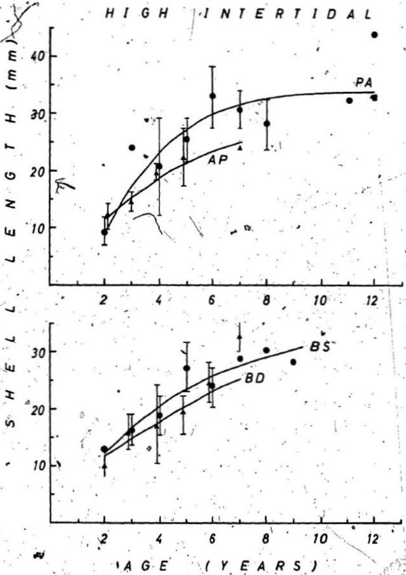

HIGH INTERTIDAL
SHELL LENGTH (mm)
40
30
20
10
2
4
6
8
10
12
PA
AP
BS
BD
AGE (YEARS)

FIGURE 9. von Bertalanffy linear shell growth curves for low intertidal Strait of Belle Isle Strait of Belle Isle *M. edulis* populations.

circles: mean lengths at north shore sites (Pte. Amour, Blanc-Sablon).
triangles: mean lengths at south shore sites (Anchor Pt., Black Duck Cove).
closed vertical bars: 95% confidence limits about means.
open vertical bars: ranges for n=2 observations.
points with no vertical bars: n=1 observations.

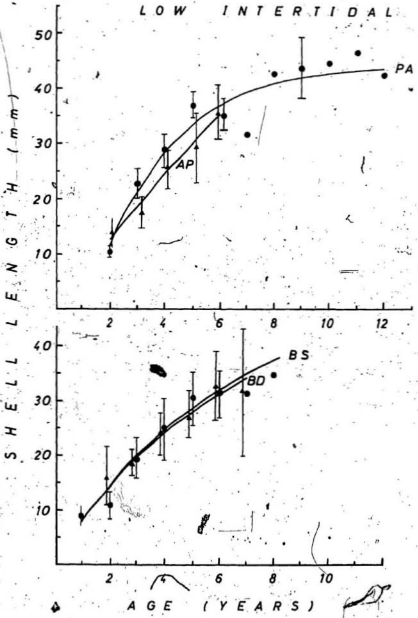

LOW INTERTIDAL
SHELL LENGTH (mm)
50
40
30
20
10
PA
AP
2
4
6
8
10
12
40
30
20
10
BS
BD
2
4
6
8
10
AGE (YEARS)

FIGURE 10. von Bertalanffy linear shell growth curves for subtidal Strait of Belle Isle *M. edulis* populations.

circles: mean lengths at north shore sites
(Pte. Amour, Blanc-Sablon).
triangles: mean lengths at south shore sites
(Anchor Pt., Black Duck Cove).
closed vertical bars: 95% confidence limits
about means.
open vertical bars: ranges for n=2 observations.
points with no vertical bars: n=1 observations.

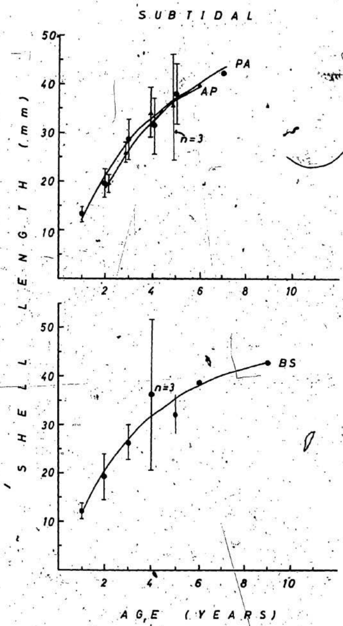

SUBTIDAL
SHELL LENGTH (mm)
50
40
30
20
10
PA
AP
n=3
2
4
6
8
10
50
40
30
20
10
BS
n=3
2
4
6
8
10
AGE (YEARS)

FIGURE 11. von Bertalanffy linear shell growth curves for intertidal Strait of Belle Isle *M. edulis*: comparisons between tidal levels.

circles: high intertidal mean lengths.
triangles: low intertidal mean lengths.
closed vertical bars: vertical 95% confidence limits about means.
open vertical bars: ranges for n=2 observations.
points with no vertical bars: n=1 observations.

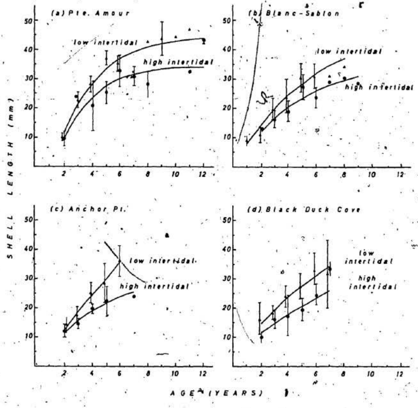

(a) Pte. Amour
low intertidal
high intertidal
(b) Blanc-Sablon
low intertidal
high intertidal
(c) Anchor Pt.
low intertidal
high intertidal
(d) Black Duck Cove
low intertidal
high intertidal
SHELL LENGTH (mm)
AGE (YEARS)
10
20
30
40
50
2
4
6
8
10
12

Figure 12. Shell morphometric data for Strait of Belle Isle *M. edulis* populations collected in August, 1981 (representative 95% confidence intervals about regression lines shown).

HEIGHT vs LENGTH

High Intertidal:			
Pte. Amour(PA)	$Y=0.458X+1.165$	$r^2=0.99$,	$n=29$
Blanc-Sablon(BS)	$Y=0.473X+1.064$	$r^2=0.98$,	$n=70$
Anchor Pt.(AP)	$Y=0.504X+0.603$	$r^2=0.96$,	$n=57$
Black Duck C.(BD)	$Y=0.496X+0.821$	$r^2=0.99$,	$n=42$
Low Intertidal:			
Pte. Amour(PA)	$Y=0.442X+1.679$	$r^2=0.98$,	$n=51$
Blanc-Sablon(BS)	$Y=0.419X+0.821$	$r^2=0.94$,	$n=40$
Anchor Pt.(AP)	$Y=0.493X+0.906$	$r^2=0.93$,	$n=43$
Black Duck C.(BD)	$Y=0.451X+1.379$	$r^2=0.96$,	$n=31$

WIDTH vs. LENGTH

High Intertidal:			
Pte. Amour(PA)	$Y=0.476X-0.411$	$r^2=0.98$,	$n=29$
Blanc-Sablon(BS)	$Y=0.458X-0.347$	$r^2=0.97$,	$n=70$
Anchor Pt.(AP)	$Y=0.415X+0.181$	$r^2=0.95$,	$n=57$
Black Duck C.(BD)	$Y=0.443X+0.255$	$r^2=0.94$,	$n=42$
Low Intertidal:			
Pte. Amour(PA)	$Y=0.454X-0.524$	$r^2=0.98$,	$n=51$
Blanc-Sablon(BS)	$Y=0.406X-0.062$	$r^2=0.95$,	$n=40$
Anchor Pt.(AP)	$Y=0.418X-0.123$	$r^2=0.94$,	$n=43$
Black Duck C.(BD)	$Y=0.465X-0.584$	$r^2=0.97$,	$n=31$

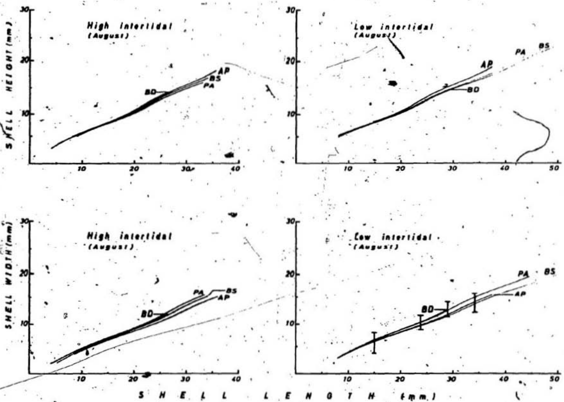
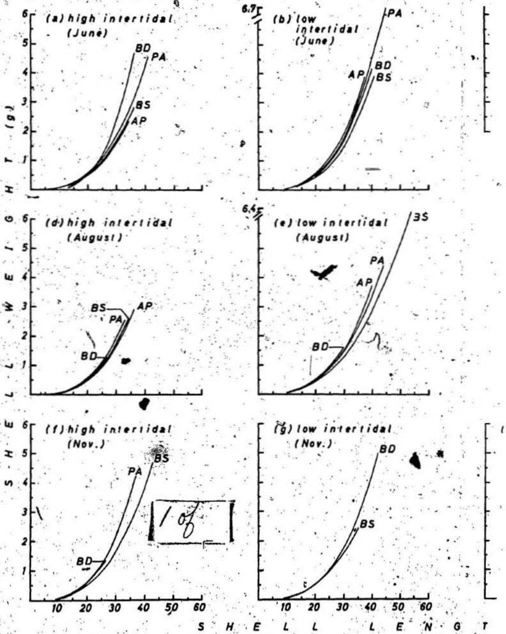

SHELL HEIGHT (mm)
SHELL WIDTH (mm)
SHELL LENGTH (mm)
High intertidal (August)
Low intertidal (August)
AP
BS
PA
BD
0
10
20
30
40
50

FIGURE 13. Shell weight vs. length allometric curves for Strait of Belle Isle *M. edulis* populations.

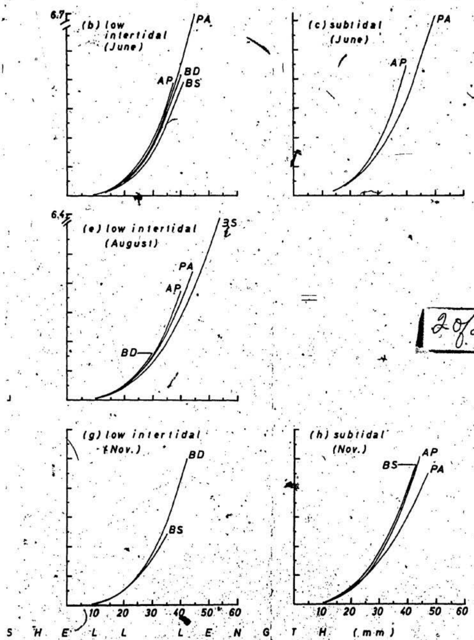
JUNE
- High Intertidal:
  - Pte. Amour, $W=0.09L^{2.917}$ $r^2=0.99$, $n=43$
  - Blanc-Sablon, $W=0.119L^{2.312}$ $r^2=0.97$, $n=23$
  - Anchor Pt., $W=0.013L^{2.737}$ $r^2=0.94$, $n=46$
  - Black Duck C., $W=0.007L^{3.75}$ $r^2=0.98$, $n=37$
- Low Intertidal:
  - Pte. Amour, $W=0.023L^{3.309}$ $r^2=0.97$, $n=50$
  - Blanc-Sablon, $W=0.041L^{3.09}$ $r^2=0.96$, $n=63$
  - Anchor Pt., $W=0.044L^{3.13}$ $r^2=0.98$, $n=50$
  - Black Duck C., $W=0.048L^{3.081}$ $r^2=0.94$, $n=58$
- Subtidal:
  - Pte. Amour, $W=0.107L^{2.804}$ $r^2=0.96$, $n=33$
  - Anchor Pt., $W=0.037L^{3.173}$ $r^2=0.98$, $n=36$

AUGUST
- High Intertidal:
  - Pte. Amour, $W=0.041L^{3.162}$ $r^2=0.99$, $n=27$
  - Blanc-Sablon, $W=0.028L^{3.24}$ $r^2=0.98$, $n=54$
  - Anchor Pt., $W=0.047L^{3.08}$ $r^2=0.97$, $n=56$
  - Black Duck C., $W=0.1L^{2.9\ 7}$ $r^2=0.98$, $n=42$
- Low Intertidal:
  - Pte. Amour, $W=0.079L^{2.9\ 9}$ $r^2=0.98$, $n=50$
  - Blanc-Sablon, $W=0.129L^{2.71}$ $r^2=0.98$, $n=54$
  - Anchor Pt., $W=0.061L^{2.99}$ $r^2=0.95$, $n=72$
  - Black Duck C., $W=0.072L^{2.95}$ $r^2=0.97$, $n=30$

NOVEMBER
- High Intertidal:
  - Pte. Amour, $W=0.035L^{3.244}$ $r^2=0.98$, $n=37$
  - Blanc-Sablon, $W=0.08L^{2.921}$ $r^2=0.98$, $n=32$
  - Black Duck C., $W=0.073L^{3.008}$ $r^2=0.97$, $n=53$
- Low Intertidal:
  - Blanc-Sablon, $W=0.129L^{2.772}$ $r^2=0.98$, $n=54$
  - Black Duck C., $W=0.064L^{3.014}$ $r^2=0.99$, $n=66$
- Subtidal:
  - Pte. Amour, $W=0.322L^{2.481}$ $r^2=0.94$, $n=55$
  - Blanc-Sablon, $W=0.137L^{2.781}$ $r^2=0.97$, $n=55$
  - Anchor Pt., $W=0.073L^{2.946}$ $r^2=0.98$, $n=50$


(a) high intertidal (June)
BD
PA
BS
AP
(b) low intertidal (June)
6.7
PA
BD
AP
BS
(d) high intertidal (August)
BS
AP
PA
BD
(e) low intertidal (August)
6.4
BS
PA
AP
BD
(f) high intertidal (Nov.)
BS
PA
BD
(g) low intertidal (Nov.)
BD
BS
SHELL WEIGHT (g)
0
1
2
3
4
5
6
10
20
30
40
50
60
SHELL LENGT

1 of


6.7
(b) low intertidal (June)
PA
BD
AP
BS
(c) subtidal (June)
PA
AP
6.4
(e) low intertidal (August)
BS
PA
AP
BD
(g) low intertidal (Nov.)
BD
BS
(h) subtidal (Nov.)
AP
BS
PA
10
20
30
40
50
60
10
20
30
40
50
60
SHELL LENGTH (mm)

2 of 2

FIGURE 14. Shell weight vs. age curves for Strait of Belle Isle *M. edulis*.

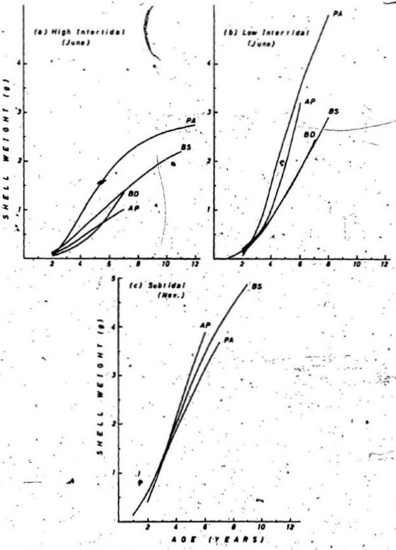

(a) High Intertidal (June)
(b) Low Intertidal (June)
(c) Subtidal (Nov.)
SHELL WEIGHT (g)
AGE (YEARS)
PA
BS
BD
AP
1
2
3
4
5
2
4
6
8
10
12

FIGURE 15. Comparison of shell weight vs. length and age growth curves between tidal levels for Strait of Belle Isle <u>M. edulis</u>.

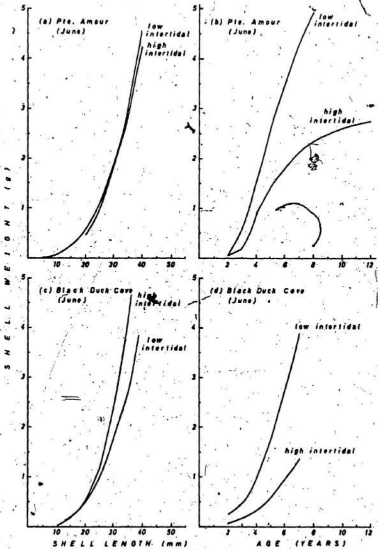

(a) Pte. Amour (June)
low intertidal
high intertidal
(b) Pte. Amour (June)
low intertidal
high intertidal
(c) Black Duck Cove (June)
high intertidal
low intertidal
(d) Black Duck Cove (June)
low intertidal
high intertidal
SHELL WEIGHT (g)
SHELL LENGTH (mm)
AGE (YEARS)
1
2
3
4
5
10
20
30
40
50
2
4
6
8
10
12

FIGURE 16. Seasonal changes in shell weight-length relationships in Strait of Belle Isle intertidal *M. edulis* populations (J-June, A-August, N-November).

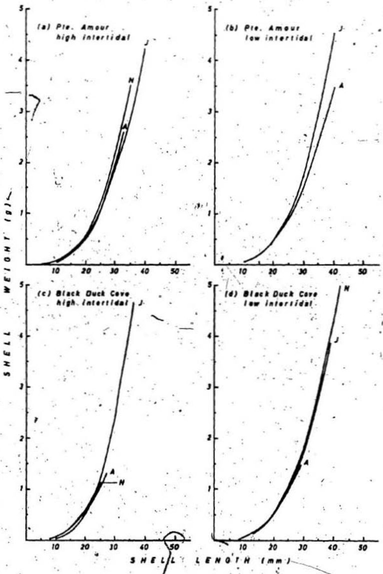

(a) Pte. Amour high intertidal
J
N
A
(b) Pte. Amour low intertidal
J
A
(c) Black Duck Cove high intertidal
J
A
N
(d) Black Duck Cove low intertidal
N
J
A
SHELL WEIGHT (g)
SHELL LENGTH (mm)
0
1
2
3
4
5
10
20
30
40
50

FIGURE 17. Meat weight vs. shell length allometric curves for Strait of Belle Isle *M. edulis* populations.

JUNE

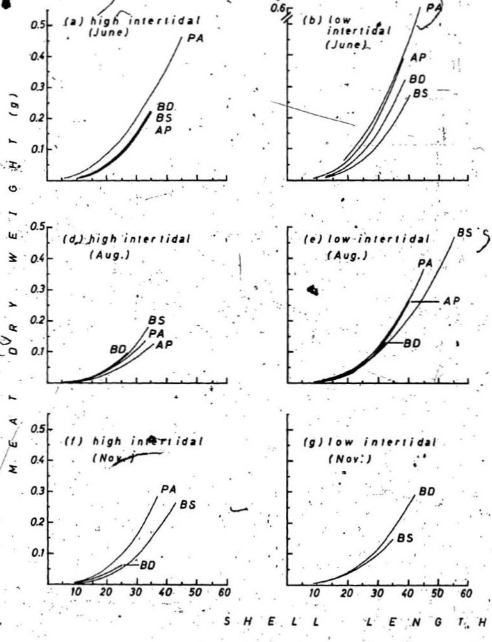
- High Intertidal:
  - Pte. Amour, $W=0.191L^{2.045}$ $r^2=0.81$, n=39
  - Blanc-Sablon, $W=0.024L^{2.576}$ $r^2=0.90$, n=19
  - Anchor Pt., $W=0.013L^{2.737}$ $r^2=0.94$, n=46
  - Black Duck C., $W=0.022L^{2.589}$ $r^2=0.90$, n=44
- Low Intertidal:
  - Pte. Amour, $W=0.037L^{2.553}$ $r^2=0.87$, n=50
  - Blanc-Sablon, $W=0.006L^{2.917}$ $r^2=0.88$, n=63
  - Anchor Pt., $W=0.014L^{2.818}$ $r^2=0.97$, n=50
  - Black Duck C., $W=0.008L^{2.991}$ $r^2=0.92$, n=53
- Subtidal:
  - Pte. Amour, $W=0.003L^{3.173}$ $r^2=0.87$, n=32
  - Anchor Pt., $W=0.019L^{2.65}$ $r^2=0.85$, n=35

AUGUST

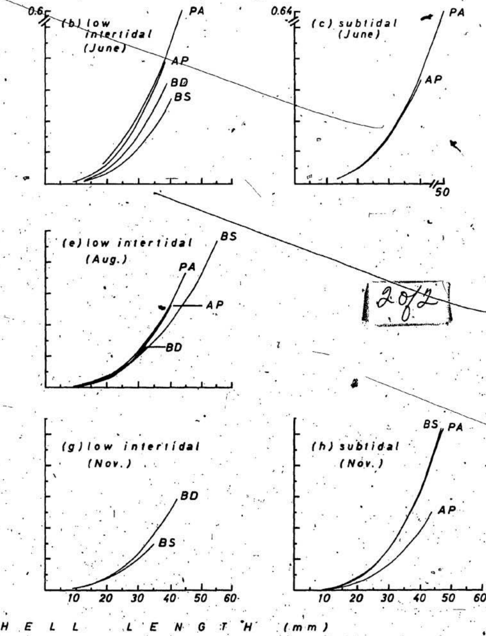
- High Intertidal:
  - Pte. Amour, $W=0.018L^{2.563}$ $r^2=0.98$, n=23
  - Blanc-Sablon, $W=0.007L^{2.88}$ $r^2=0.89$, n=31
  - Anchor Pt., $W=0.016L^{2.5}$ $r^2=0.77$, n=47
  - Black Duck C., $W=0.013L^{2.71}$ $r^2=0.88$, n=35
- Low Intertidal:
  - Pte. Amour, $W=0.008L^{2.82}$ $r^2=0.97$, n=44
  - Blanc-Sablon, $W=0.015L^{2.58}$ $r^2=0.96$, n=49
  - Anchor Pt., $W=0.003L^{3.15}$ $r^2=0.9$[illegible], n=42
  - Black Duck C., $W=0.003L^{3.09}$ $r^2=0.94$, n=21

NOVEMBER

- High Intertidal:
  - Pte. Amour, $W=0.017L^{2.658}$ $r^2=0.94$, n=34
  - Blanc-Sablon, $W=0.004L^{2.961}$ $r^2=0.95$, n=30
  - Black Duck C., $W=0.029L^{2.376}$ $r^2=0.93$, n=53
- Low Intertidal:
  - Black Duck C., $W=0.014L^{2.665}$ $r^2=0.97$, n=66
  - Blanc-Sablon, $W=0.022L^{2.473}$ $r^2=0.93$, n=75
- Subtidal:
  - Pte. Amour, $W=0.007L^{2.981}$ $r^2=0.97$, n=54
  - Blanc-Sablon, $W=0.006L^{2.969}$ $r^2=0.97$, n=55
  - Anchor Pt., $W=0.005L^{2.877}$ $r^2=0.96$, n=51


MEAT DRY WEIGHT (g)
(a) high intertidal (June)
PA
BD
BS
AP
0.6
(b) low intertidal (June)
PA
AP
BD
BS
(d) high intertidal (Aug.)
BS
PA
BD
AP
(e) low intertidal (Aug.)
BS
PA
AP
BD
(f) high intertidal (Nov.)
PA
BS
BD
(g) low intertidal (Nov.)
BD
BS
0.1
0.2
0.3
0.4
0.5
10
20
30
40
50
60
SHELL LENGTH

1 of


0.6
(b) low intertidal (June)
PA
AP
BD
BS
0.64
(c) subtidal (June)
PA
AP
50
(e) low intertidal (Aug.)
BS
PA
AP
BD
(g) low intertidal (Nov.)
BD
BS
10
20
30
40
50
60
(h) subtidal (Nov.)
BS
PA
AP
10
20
30
40
50
60
HELL LENGTH (mm)

2of2

FIGURE 18. Meat weight vs. age growth curves for Strait of Belle Isle, intertidal *M. edulis*.

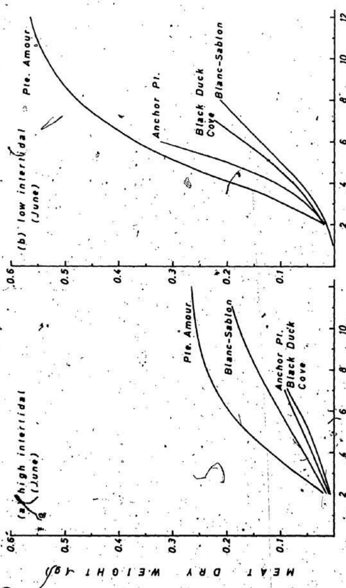

(a) high intertidal (June)
Pte. Amour
Blanc-Sablon
Anchor Pt.
Black Duck Cove
(b) low intertidal (June)
Pte. Amour
Anchor Pt.
Black Duck Cove
Blanc-Sablon
0.6
0.5
0.4
0.3
0.2
0.1
2
4
6
8
10
12
MEAT DRY WEIGHT (g)
AGE (YEARS)

FIGURE 19. Comparison of meat weight vs. shell length and age between tidal levels for Strait of Belle Isle M. edulis populations.

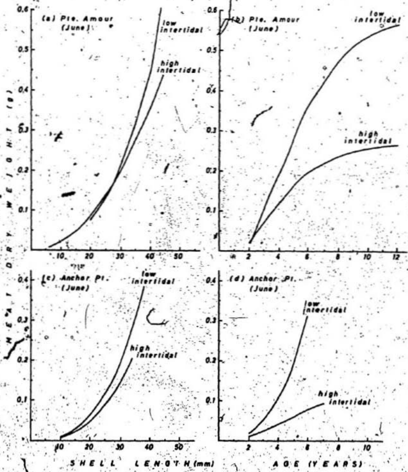
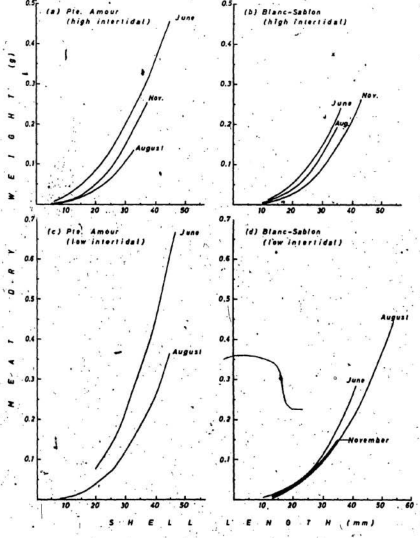

MEAT DRY WEIGHT (g)
(a) Pte. Amour (June)
low intertidal
high intertidal
0.6
0.5
0.4
0.3
0.2
0.1
10
20
30
40
50
(b) Pte. Amour (June)
low intertidal
high intertidal
2
4
6
8
10
12
(c) Anchor Pt. (June)
low intertidal
high intertidal
0.4
0.3
0.2
0.1
10
20
30
40
50
(d) Anchor Pt. (June)
low intertidal
high intertidal
2
4
6
8
10
SHELL LENGTH (mm)
AGE (YEARS)

FIGURE 20. Seasonal changes in meat weight for intertidal *M. edulis* populations.


(a) Pte. Amour (high intertidal)
June
Nov.
August
(b) Blanc-Sablon (high intertidal)
June
Aug.
Nov.
(c) Pte. Amour (low intertidal)
June
August
(d) Blanc-Sablon (low intertidal)
August
June
November
MEAT DRY WEIGHT (g)
SHELL LENGTH (mm)
0.1
0.2
0.3
0.4
0.5
0.6
0.7
10
20
30
40
50
60

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APPENDIX A

Formation of the Shell Internal Growth Line in Mytilus edulis

Lutz (1976) conclusively demonstrated that the major, repeating microgrowth increment in M. edulis is annual, and occurs in the inner nacreous shell layer. Lutz and Rhoads (1977) point out that microstructural growth increments within nacre have only rarely been reported. Instead, internal shell growth increments have been studied in the outer, prismatic shell layer (e.g. Pannella and MacClintock, 1968; Barker, 1970).

Internal growth lines in bivalves which have an annual periodicity can be classified into one of two categories, winter or winter/spring deposition (e.g. Panope generosa :Shaul and Goodwin, 1982; Geukensia demissa :Lutz and Rhoads, 1977; Mya arenaria: MacDonald and Thompson, 1980) and deposition at the time of spawning (e.g. M. edulis:Lutz, 1976; Mercenaria mercenaria :Kennish and Olsson, 1974; Arctica islandica and Spisula solidissima :Jones, 1980). In the case of A. islandica and S. solidissima, the coincidence of appearance of the growth line and spawning is most striking as the spawning periods occur in different seasons in these two species. In my study the timing of deposition of the internal growth line coincided with the spawning season and rising water temperatures. Variation in the timing of growth line deposition within populations was consistent with the spawning period, within mussel populations in general, staggered about a maximum. Furthermore, in contrast to Maine mussels which deposit a growth line in mid-June, during the spawning season, Strait of Belle Isle mussels deposit a line approximately one month later, but again during the spawning season.

Despite the voluminous literature pertaining to all other aspects of the biology of *M. edulis*, the literature related to its internal growth line is depauperate. Barker (1970) maintained that it was impossible to factor out either temperature or spawning activity to arrive at the true cause for growth line deposition. In accordance with other growth line studies (e.g. Barker, 1970), in my study, spawning activity coincided with rising (near peak) surface water temperatures.

The observation of reduced shell growth during the reproductive period is not new. Bruce (1926) observed an almost complete shutdown of shell growth, throughout and for some time after the actual spawning period, and it was not until later that high summer temperatures and a reduced demand by gonadal material allowed renewal of shell deposition. Coe and Fox (1942) postulated that a mid-summer decrease in shell growth rate might be attributed to the spawning cycle. Mussels are stressed, in energy or metabolic terms, because of gametogenesis (e.g. Bruce, 1926; Pickens, 1965; Bayne, 1973; Gabbott and Bayne, 1973; Dare and Edwards, 1975). I suggest that what little evidence exists indicates that the formation of the internal growth line in *M. edulis* may be the result of an energy or metabolic "shunt" from the shell-building process to the maturing gonad during accelerated gametogenesis, possibly during the vitellogenic (maturation) phase.

Lutz (personal communication) claims that the above hypothesis is similar to what he suspects may be causing growth line formation in *M. edulis*, and comments that: "...During gametogenesis, oxygen may be "shunted" to the mantle tissues. This in turn could result in increased utilization of anaerobic pathways in the mantle tissues, resulting in production of acidic end products that could actually be responsible for shell dissolution." This then would be in accordance with the general anaerobic theory of growth line formation (Lutz and Rhoads, 1977).

After examining approximately 500 shell thin sections during the course of my study, it has become apparent to me, as it has to others (Pannella and MacClintock, 1968), that intertidal mussels typically deposit a more clearly defined growth line than do subtidal mussels. Mussels which are able to feed constantly (subtidal) likely would not be stressed as much, in energy terms, during gametogenesis (due to a more constant food supply or better stored energy reserves) as would mussels with less time to feed (intertidal). Subsequently, the energy shunt away from shell growth would be less in these mussels than in intertidal mussels, with the resulting less pronounced growth line found in subtidal mussels. An exception to this occurred in my study at the shallow (2 m depth) subtidal, Anchor Pt., site, where the mussel population showed very pronounced growth lines. Whereas all the other sites occurred on exposed coastline, this latter site was in a sheltered locality. While the low intertidal, exposed-coast populations are densely aggregated, and characterized by prominent internal growth lines, the subtidal populations are typically not as dense. In the one sheltered locality, however, mussels were very dense, and I suggest that this high density, combined with the shallow depth of the water, may result in a situation where food is limiting to growth. Thus at the time of vitellogenesis, shell growth is markedly slowed down, as in the intertidal populations, with a corresponding well- defined growth line. Kautsky (personal communication) questions whether or not growth line distinctiveness could best be explained in terms of energy balance rather than by food abundance. He postulates that energy supplied during the reproductive period is probably channelled into gonad development, resulting in low shell growth despite abundant food (Kautsky, 1982a). He goes on to say that this energy shunt, combined with temperature differences (air and water) between intertidal and subtidal zones and the corresponding effect upon metabolic rate, might explain the differences in growth line distinctiveness. Still another explanation to explain differences in growth line distinctiveness is put forward by B. L. Bayne (personal communication). Some recent evidence that he has for *M. edulis* and that Griffiths (1977) has for *Choromytilus* indicates that the higher the tidal level inhabited, the greater the reproductive effort.