Small-scale variations in mussel (*Mytilus* spp.) dynamics and local production[1]

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ABSTRACT

A mussel bed was sampled monthly at four intertidal levels (mid: 2.15; mid-low: 1.65; low: 1.2 and sublittoral fringe: 0.7 m from chart datum) from July 1979 to July 1980 at Pointe-Mitis in the St. Lawrence estuary. Our results show a strong spring reduction of abundance (both in density and biomass), which suggests that the mussel bed was being degraded. Community perturbation was attributed to ice scour. Partial reestablishment of the mussel bed (all age classes) was observed during late spring and early summer and occurred mainly at the mid-low intertidal level. Changes in the size structure of the mussel bed with level suggest that the annual windstorm regime may be an important factor in the dynamics of the bed. Mean body mass decreased at the three lower shore levels but increased at the highest shore level. Overall, net secondary production (assessed by the increment summation method) was negative due to the decrease in mean body mass. Annual production (kJ m^{-2} yr^{-1}) from the mid intertidal level to the sublittoral fringe were respectively 1130, - 4072, - 4013 and - 3258 while P/B ratios (yr^{-1}) were 0.17, - 0.69, - 0.50 and - 0.45. The calculated production and the productivity (potential production) are compared and used to provide insight about the condition of the mussel bed.

KEYWORDS: secondary production, population dynamics, productivity, small-scale, intertidal, mussel bed.

INTRODUCTION

Population dynamics (recruitment, growth and mortality) are controlled by local processes in many benthic communities (Sousa, 1984; Underwood and Petraitis, 1993; Guichard and Bourget, 1998; McKindsey and Bourget, 2000; Jenkins et al., 2001). Intertidal and shallow communities are strongly affected by physical disturbances such as wave action and winter storms (Grant, 1977) and, for subarctic and cold temperate regions, ice scouring and freezing (Dayton et al., 1969; Dayton et al., 1970; Archambault and Bourget, 1983; Bergeron and Bourget, 1984; Bourget et al., 1985; Heine, 1989) are major factors structuring the community. Exposure to waves, ice scouring, freezing, desiccation, exposure to sunshine, etc., all vary with intertidal level. In addition, duration of immersion along this gradient is a major factor affecting food availability, recruitment and growth (Suchanek, 1978; Eckman, 1983; Seed and Suchanek, 1992) resulting in different local biomass.

Populations may be compared using local abundance (e.g. biomass, density). To provide insight about the processes involved, biomass data are usually complemented with growth data. Studying secondary production, however, would give a synthesis of local mortality, growth rate, individual body mass, recruitment, population density and biomass and is a much more complete indicator of population dynamics than mean biomass and growth rate alone. Indeed, production (the estimate of the incorporation of organic matter or energy per time unit) gives a comprehensive representation of the "success" of a population as it can be used to define its functional importance at the community or ecosystem levels (Benke, 1993) as it is fundamental in the trophic linkage of compartments. Since production is a dynamic parameter, it therefore is an important indicator of the population condition (i.e. population state in terms of individual growth, as well as the level of density and biomass and their variation.) The term "production" refers to the actual rate of incorporation of organic matter or energy whereas "potential production" or "productivity" refers to production under the theoretical steady state conditions in which there are no changes in overall biomass and age/size frequency from year to year (sensu Davis, 1963; Crisp, 1984). This latter situation, however ideal, rarely occurs in

nature (Rigler and Downing, 1984) and a clear unsteady state population far from this ideal condition could change the pattern of an expected production. Reviews of secondary production calculation (Winberg et al., 1971; Waters, 1977; Crisp, 1984; Rigler and Downing, 1984) describe basic methods to assess production with steady populations. However, the application of general principle of

5   calculation must be adapted to the specific properties of each species and environment (Winberg et al., 1971). Dealing with unsteady and non-synchronic populations may lead to some difficulties in calculating production and productivity.

Intertidal populations of mussels are valuable in showing how the dynamics (growth and production)

10   can differ substantially over very short spatial scales due to the strong environmental gradient of this environment. Indeed, a negative correlation has been observed between mussel (Mytilid) production values and shore level (Griffiths, 1981a; 1981b). An intertidal subarctic mussel population is used here to highlight some aspects encountered in calculating and interpreting productions when working with populations in an unsteady state. The objectives of this paper are (1) to describe the variations of

15   abundance within a subarctic mussel population at different shore levels, (2) to illustrate how individual growth and secondary production can vary locally among levels, (3) to examine the significance of a negative net production as a condition indicator of the population, and (4) to discuss the use of production and productivity in interpreting such unsteady state populations.

20   **METHODS**

Field sampling methods

The study was located at Pointe-Mitis (Fig. 1), an exposed shore on the south shore of the St. Lawrence estuary, Québec, Canada, where a large mussel bed occurs on a relatively uniform mudflat that gently sloped from the midintertidal to the subtidal levels. Data (from M. Bousquet, M. Fréchette

25   and E. Bourget) were collected in 1979-80 in the context of a larger study but have not previously been published except for the general trends in density and biomass (Fig. 6 in Bourget et al., 1985).

Here we analyse these data to examine the relationship of population dynamics and production over a small spatial scale. As for the winter sampling, we have not found any other winter production data based on winter sampling in the literature for the subarctic environments and therefore this year-based sampling design, which included winter samples, is unique.

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Three intertidal sampling zones (15 m X 30 m, parallel to the shore line) in the mussel bed (a mixed assemblage of *Mytilus edulis* and *M. trossulus*, hereafter *Mytilus*) area were sampled monthly from July 1979 to July 1980 (13 months) at three different shore levels (mid intertidal: 2.15 m above 0 chart datum; mid-low intertidal: 1.65 m and low: 1.2 m). Overall tidal range at the site is 4.5 m. Distance

10   between each sampling zone was 12 m. An additional sampling zone, 4 m below the lower zone, was a "transect" (2 m X 30 m) located in the sublittoral fringe (0.7 m from the datum); it was sampled from July 1979 to June 1980 (12 months). No sampling was carried out in December 1979 and February 1980 due to ice cover in the sublittoral fringe level. Within each zone, ten haphazardly positioned quadrats (10 X 10 cm) were collected on each sampling date. Due to ice cover, only parts of the bed

15   were accessible during winter months (January to April), but by using natural points of reference, we could still sample from the same general zones as when the bed was free of ice. The sampling scheme was, however, different as sampling effort was restricted to just the accessible parts of the zones. Therefore deviations in the sampling design probably influenced the winter results to a certain extent, but biases could not be determined *a priori*. However, comparable year-based results (not shown)

20   were obtained whether we considered or not these winter months. All samples were washed through a 1-mm sieve and sorted in the laboratory.

Age class was determined from the number of winter growth rings, a method which has been validated using shell sections in mussels from the northeastern United States (Lutz, 1976). Cossa and Bourget

25   (1985) have shown the validity of external winter growth marks in the St. Lawrence subarctic system (including Pointe-Mitis site) using an independent method, that of shell sections. The reduced growth

of mussels during the winter period, which includes 3 to 4 months of ice cover, makes a pronounced annual winter mark due to arrest of growth on the shell surface. Ageing methods using shell external growth rings have also been used for growth studies on mussels in subarctic or arctic environments (Sukhotin and Maximovich, 1994; Littorin and Gilek, 1999; Millstein and O'Clair, 2001), as well as

5   for secondary production determination (Thompson, 1984) or energy flow studies (Sukhotin and Poertner, 2001). Because few individuals >6 yrs-old were found we pooled older mussels together.

Individuals in each age class were counted and tissue (shell-free) weighed ($\pm$ 0.0005 g) together to determine biomass. All densities and tissue weights (g wet weight; gWW) were calculated by m^{-2}. No

10   separate evaluation of gamete production was done as the gonad tissue is distributed throughout the mantle tissue, making biomass estimates approximate at best. Therefore all changes in body mass were considered to be somatic production.

Calculation of secondary production

15   Annual secondary production of mussels for each level was first calculated using two cohort-based methods, the increment summation (IS) and removal summation (RS). These two methods use measures of mortality and growth estimated from changes in densities (N) and individual body mass (W) variables (see details in Crisp, 1984). W was calculated by dividing the biomass of each age fraction by its density.

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Production for each age class by increment growth summation (P_{is}) is given by the equation:

$$P_{is} = (N_t + N_{t+1})/2 \bullet (W_{t+1} - W_t) \tag{1}$$

Confidence intervals were calculated using the non-parametric bootstrap method (Efron and Tibshirani, 1993) to show the range of the calculated production (as suggested by Morin et al., 1987;

25   Brey, 1990). The median of a thousand-production computation (IS method) was carried out using, for each computation, 10 random quadrats chosen (with replacement) among those

available. The 25th and 975th results of the ascending matrix represent the two tails (p [2.5] and p [97.5]) of the true distribution.

RS production (P_{rs}) was computed using the mortality increment for each age class as expressed by the Elimination equation:

Elimination = (N_t - N_{t+1}) • (W_t + W_{t+1})/2 (2)

P_{rs} = Elimination + residual biomass. Residual biomass is equal to net change in mean biomass which is the mean biomass of the last sampling date minus the mean biomass of the first sampling date. Total production is equal to the sum of the production of each age class. To facilitate the computation by both cohort-based methods, sampling dates were removed in calculations where mean density of any age class equalled zero. This assumption could lead to a small bias.

The potential production (productivity) of the mussel bed was also estimated by the body mass growth increment from one cohort to the next (up to age class >6, with addition of the 0-yr class biomass) using all pooled sampling dates assuming steady state of the age-frequency structure and a steady mean annual body mass of each cohort from year to year (a pre-requisite condition to estimate productivity).

RESULTS

Biomass and density

Higher values of mean mussel abundance (density and biomass) were observed in the sublittoral fringe and in the low intertidal zones than in the mid-low and mid intertidal zones (Table 1). Old mussels (>2 years-old) numerically dominated the mid and mid-low intertidal levels compared to other levels, especially the sublittoral fringe, where the recruit (0-yr class) densities were high. Density of recruits was inversely related to shore level. The 0-yr class was well represented at the beginning of the study (July 1979) and its abundance remained high or peaked during the late summer and fall. In contrast,

numbers fell dramatically over the winter, especially from February to April (Fig. 2i, j), and no new recruitment of a 0-yr class was observed during summer 1980. A sharp decrease in density and biomass was also observed across all other age classes for each intertidal level except at the mid-low intertidal where only a decrease in biomass was measured. This massive mortality (and/or emigration) was much higher in the sublittoral fringe and the low intertidal levels (Fig. 2) than in the upper levels. Although a restoration of the age distribution in abundance was observed at the mid-low intertidal level (Fig. 2c, d), a general lack of synchronicity and cohesion of the mussel abundance of each age fraction indicate a strong departure of the steady state for this mussel population. After the large decrease of abundance in the spring, the mussel population structure (density and biomass) recovered from April to June (Fig. 2c, d) in the mid-low intertidal level while little recolonisation was observed in the low and sublittoral fringe levels (Fig. 2e, f, g, h).

Growth and production

The body mass of individual *Mytilus* generally increased from July to September 1979 while it decreased from December to April 1980 (Fig. 3a, c, e, g). Highest body mass values (age classes >3 yrs old) were found in the lower part of the intertidal while smaller values were observed in the two upper intertidal levels (Fig. 4). Strong growth was observed between April and May 1980 followed by a decrease in body mass probably associated with spawning. The 0-yr class (July 1979 settlement) was considered as the same age class during the survey for production calculation purposes as no new settlement has been observed in July 1980. The population in the sublittoral fringe had a period of negative monthly net production from October to April. No clear pattern was observed for other levels (Fig. 3b, d, f). During the year of survey, negative values of production were observed especially for the 3 to 6 age classes while a little positive production was observed for the first two age classes and the older mussel age class (>6 yr) (data not shown). Both methods for production estimation (IS and RS) gave the same results. Annual net production (gWW m^{-2} yr^{-1}) varied among intertidal levels;

estimates were 923, - 3325, - 3277, and - 2260, in the mid, mid-low, low intertidal and sublittoral fringe levels, respectively (Table 1). P/B (yr^{-1}) were 0.17, - 0.69, - 0.5, and - 0.45.

Negative net production values were observed for both the low and mid-low intertidal levels while positive values were observed at the highest level (Table 1). Elimination values were always higher than the production values except for the mid-low intertidal level (Table 1). These results are characteristic of a mean biomass loss (when $P < E$) and a mean biomass gain (when $P > E$) in the populations. The population of the mid-low intertidal level had a significantly lower production value than that of the high level as shown by the bootstrap confidence intervals while there was no significant difference between the IS secondary production at the other levels (Table 1). When data from all levels were pooled, the annual production (using IS), mean annual biomass, mean annual density, and P/B ratio of the entire mussel bed were respectively – 1418 gWW m^{-2} yr^{-1}, 5781 gWW m^{-2}, 10557 ind. m^{-2}, and - 0.25 yr^{-1}.

The potential production or productivity values (gWW m^{-2} yr^{-1}), calculated by the growth increment of the mean annual body mass between each age class and in assuming a steady state of the age structure, were 2028, 2198, 4023 and 5274 and the potential P/Bs (yr^{-1}) were 0.38, 0.45, 0.61 and 0.89 respectively in the mid, mid-low, low intertidal and sublittoral fringe levels.

DISCUSSION

Our results show that at the time of sampling the *Mytilus* population at Pointe-Mitis was in a non steady state. Indeed, except for the mid-low intertidal level, we observed an overall decrease in density and biomass and we did not observe a balanced budget of body mass over the yearlong period of the study. The mean body mass loss during the winter and spring 1980 was definitively higher than the gain observed in summer and autumn 1979. Furthermore, within the same mussel bed, the abundance (density and biomass) varied substantially among intertidal levels. The secondary production values

were negative for the three lower levels (sublittoral fringe, low and mid-low intertidal) and showed significantly different values from adjacent levels in the same mussel bed. This mussel bed still remains at Pointe-Mitis, which suggests there must have been positive production following our survey to maintain a standing stock. Indeed, mussel dominance can persist on rocky shores providing growth is sufficient to compensate for mortality and the balance between growth and mortality and/or emigration processes remains positive (Petraitis, 1995). Although from this study it is impossible to determine the exact mechanisms responsible for the observed population dynamics, it seems that ice scouring events during spring may have been involved in abundance, growth and production changes among intertidal level zones. From our survey, it is clear that the mussel bed was dismantling itself during the survey period.

Variation in biomass and densities

The strong variations in both biomass and density were observed mainly during spring and were probably related to the recurrent ice scouring perturbation events. Ice scouring is the principal physical factor affecting the structure of the blue mussel bed at Pointe-Mitis (Bourget et al., 1985) and the intertidal community of the St. Lawrence (Bergeron and Bourget, 1986). Even if ice cover can protect the mussel bed against the erosion effects of wave action (Bourget et al., 1985), ice block movement can disturb mussel bed. Predation is known to be a factor affecting mussel abundance especially in the low intertidal (Seed, 1969) but it is negligible in the intertidal zone in St. Lawrence estuary even during summer and is certainly not a major factor influencing mussel populations (Guichard and Bourget, 1998; McKindsey and Bourget, 2000). Indeed, the mussel population studied at Pointe-Mitis during the period of study (1979-80) was free from predators such as starfish (*Leptasterias polaris*), crabs (*Cancer irroratus*) and dogwinkle (*Nucella lapillus*), few eider ducks have been observed feeding on the mussel bed (Fréchette and Bourget, 1985). Mussels constitute a very small part of their diet (<1%) in the St. Lawrence estuary (Cantin et al., 1974).

Mussel bed reorganization

Trends in mussel abundance (density and biomass) suggest numerous emigration and immigration movements in the mussel bed, particularly during spring. Gaps in the mussel bed due to ice scour perturbation can destabilize the mussel matrix and cause emigration thereby increasing the variance-to-mean ratio of the population. The seasonal abundance patterns suggest a passive emigration from the low levels (low level and sublittoral fringe) to the subtidal level and from the mid intertidal to the mid-low intertidal level (Fig. 2). Our results (Fig. 2c, d) suggest a rapid recovery of mussel abundance at the end of spring. Recolonisation by *Mytilus californianus* took 2 yrs to more than 8 yrs to reach total cover of the substrate (Seed and Suchanek, 1992) in Washington State. Up to 6 yrs was necessary for the recovery of mussels in Nova Scotia following a strong ice scour event in the low intertidal level (Minchinton et al., 1997). In our study, recolonisation occurred in late spring/early summer and affected all age-classes. Thus, other mechanisms than the usual recruitment of 0-yr class individuals are involved in the St. Lawrence Estuary, possibly the passive redistribution by ice scouring or water motion (currents, waves). The presence of many ice rafts with mussels attached to their underside together with the clearing of the mussel bed at the intertidal level during the survey in late spring (Bourget, pers. obs.) are indicative of the ice scouring effects. These ice rafts may also be involved in relocating mussels within the bed.

The redistribution of mussels in late spring could result from wave and storm actions in a process analogous to that known to influence the geomorphology of beaches. Indeed, in beach dynamics, seasonal hydrodynamics explains the passive redistribution of pebbles and cobbles. High energy storm-wave events, associated with the autumn and winter seasons, remove sediments from the upper shore and deposit them in the low shore and subtidal level (Nordstrom, 1992), thereby changing the beach profile. Restoration of the beach profile by sediment accretion occurs during the non-storm period (e.g. summer). This passive erosion-deposition model could also act on individual mussels detached from the bed. We have not directly evaluated emigration/immigration between levels, but we

hypothesize that the juvenile and adult mussel immigration at the mid-low intertidal and low intertidal levels (Fig. 2c,e) from April to June originate from mussels from the subtidal area, which would have been deposited there during January to March when they were dislodged from the intertidal level. In the St. Lawrence estuary, it has been clearly demonstrated experimentally that, on a cleared substratum a new mussel community composed of different age classes, including adults, is assembled during one summer (McKindsey and Bourget, 2001).

Factors affecting mussel growth

Generally, growth rather than mortality is the primary determinant of *Mytilus edulis* production (Mallet and Carver, 1989). The loss of body mass from some age classes throughout winter and spring recorded at Pointe-Mitis led to negative annual production estimates using a classical cohort based method. The negative values of annual production observed for the 2 to 6 age classes, coupled with their numerical abundance explained the key role of these age classes in the negative annual production for the whole bed. Body mass loss during winter has been observed for many intertidal populations of mussels (e.g. Dare, 1976b) and Tellinids (Ansell and Trevallion, 1967). A general decrease of adult body mass occurs during spawning, but the spawning period of mussels (gamete release) occurs from late May to August in the St. Lawrence (Bourget and Lacroix, 1973; Poirier and Myrand, 1982), slightly later than in some regions of Europe (Dare and Edwards, 1975; Dare, 1976b), and could explain some of the negative production observed during May and June. Gamete mass can reach up to 50% of the whole body mass, and during spawning, 80% of gamete mass can be lost (see Gosling, 1992). The reproductive tissues may account for over 50% of the body mass without shell, and up to 90% for the larger mussels (Griffiths, 1981a; Seed and Suchanek, 1992). Dare and Edwards (1975) observed decrease of soft-tissue mass up to 55% from October to March in a sublittoral mussel bed in North Wales. In this study the gamete production was not evaluated, but since the body mass decreased in all age classes, it suggests a massive utilization of food reserves by the mussels during late autumn and winter. Somatic growth in mussels is high in summer, linked to the period of

maximum phytoplankton production (mid-June to early September Demers et al., 1987), low in winter due to low water temperatures and low food quantity and/or quality (Alunno et al., 2000). In natural populations of mussels, production could also be limited by physiological stress (Koehn and Bayne, 1989), primary space (Paine and Levin, 1981) and predation (Dare, 1976b; Gardner and Thomas, 1987), but food availability is probably the major factor affecting growth (Jørgensen, 1979; Fréchette and Bourget, 1985; Gosling, 1992) which is also related to the emersion duration of a given intertidal level.

Mixed nature of the mussel bed

Mytilus edulis and *M. trossulus* are two species coexisting in the St. Lawrence gulf and estuary and their proportion can vary in space and in time (Thomas et al., 2003). In our population, the proportions of both species as well as hybrids were unknown in 1979-80, but unpublished data from our site have shown that, in 1986, there were 28% of *M. edulis*, 20% of hybrid and 52% of *M. trossulus* (R. K. Koehn, pers. comm.). It has been shown that *M. edulis* and *M. trossulus* have slight differences in growth rate (length and shell weight are both slightly higher in *M. edulis* than in *M. trossulus*) rather than in tissue weight (Mallet and Carver, 1995). Our production estimates did not include the shell. Frequencies of the two species in the St. Lawrence system show no clear patterns of distribution with wave exposure, tidal height or among microhabitats (Moreau, Tremblay and Bourget, in prep.) Hence, we cannot determine individual species growth and survival profiles and species secondary production in mixed mussel populations (Mallet and Carver, 1993) (see also Archambault et al., 1999; Hunt and Scheibling, 2001, for studies on mortality and recruitment of mixed mussel populations). We assume that the ice scouring and other physical factors similarly affect both *M. edulis* and *M. trossulus*.

Actual production and potential production (productivity)

The *Mytilus* P/B ratios (production calculated by increment summation) vary substantially (from - 0.69 to 0.17 yr^{-1}; cf. Table 1) reflecting variability in the mussel bed condition among levels. These actual

production values can be used as a complementary indicator of population condition to the seasonal variation in population density and biomass. They give additional information about the unbalanced body mass and the non-synchronized growth and recruitment over the year of survey. However, a difference between the actual production and the potential production (which assumes a steady state) gives an insight to the departure from the steady state. According to this, for example, the mid intertidal population showed the lowest departure from the steady state (actual P/B and potential P/B ratios 0.17 and 0.38 yr^{-1}). The difference between the value of actual production and elimination (see Table 1) for the same population is best explained by the fact that growth and mortality do not occur at the same period during the year (Bachelet, 1982).

The cohort-based method used here, instead of other empirical methods (e.g. empirical equations, P/B ratios), allows an assessment of the actual population structure within the mussel bed. A thorough survey of the literature from 1970 to 1999 (15 major journals) shows that few published studies on marine benthos production (4 of 547 assessments) have revealed a negative net value of secondary production assessed by cohort and size-based methods (unpublished data from authors). Rarely has a negative net P/B ratio been reported in the literature. When the population dynamics is not in a steady state, researchers often assess productivity instead of the actual production. A somatic production to biomass ratio (yr^{-1}) of - 0.04 was observed for the bivalve *Scrobicularia plana* (Bachelet, 1982), - 0.25 for the bivalve *Macoma balthica* (Wolff and de Wolf, 1977), - 0.12 for the limpet *Patella vulgata* (Workman, 1983) and - 0.002 for the echinoderm *Echinocardium cordatum* (Warwick et al., 1978). Those negative production values came from an negative body mass growth of aged populations probably linked to the utilization of food reserves and the spawning period (e.g. Bachelet, 1982; Workman, 1983) with little or no new recruitment (e.g. Wolff and de Wolf, 1977; Warwick et al., 1978). However, those negative net P/B ratios, if associated to an appropriate sampling program, can reflect profound restructuring of the population.

The utilisation of P/B ratios should be used with great care for the productivity assessment of natural populations (Downing, 1984; Benke, 1993). For obvious reasons, our negative productions assessed by classical methods should be used only as an indicator of the state of the mussel bed and not as a predictive tool. If the gamete production were measured from body mass, our production results could differ. Nevertheless, this study underlines the usefulness of production measurements to show differences in population dynamics between levels. Our results show a significant higher production in the mid intertidal level than in the mid-low intertidal level. This difference between two adjacent intertidal levels, separated by only 12 m, seems to be related to a small decrease in body mass during spring in the mid intertidal. We also show, as recommended by Brey (1990), that the bootstrap confidence intervals can be a useful tool to compare production among populations from different levels.

Mytilid production estimates from various environments exhibit a wide range of values (Table 2). Results from Dare (1976a) were exceptionally high (37030-66971 kJ m^{-2} yr^{-1} respectively) due to the short life span (3 yrs) and large density of their mussel beds. Our calculated annual potential productions, which, assuming the mean annual body mass of each age class representative of a steady state, are comparable to other assessments conducted at the same latitude (Table 2). Potential production to biomass ratios (from mid intertidal to sublittoral fringe levels: 0.38, 0.45, 0.61 and 0.89 yr^{-1}) are also in the same range as the P/B ratios from temperate regions and show similar gradients along the vertical axis as those found by Griffith (1981a). The mobility of some intertidal organisms such as polychaete species can also affect the secondary production when juveniles with a high growth rate migrate to other parts of the beach and affect local P/B ratios (Sarda et al., 2000). Changes in potential production to biomass ratios with shore level can also reflect the high proportion of young age classes (0- to 3-yr classes), which had a larger growth rate and age-specific P/B ratios in the two lowest shore levels than the two highest ones. The differences in P/B ratios between two populations

of the same species may be related to the age structure, high P/B ratios being related to young populations (Warwick, 1980).

Conclusion

Our results illustrate the difficulties of assessing benthic secondary production. Despite the fact that we used (1) an easily accessible intertidal population, (2) a species with well-known biological characteristics, (3) a quasi-monospecific community, (4) an intensive well structured monthly sampling program, the large spatial and temporal variability in density and winter body mass loss may complicate the determination of the annual production estimate, especially when growth and mortality processes are not synchronized over the year. Depending on calculation method used (cohort-based and potential production or productivity) the estimates could substantially be different. However, the question extrapolating the estimates of production of an unstable population remains open. The fact that very few negative results have been published so far suggests that many authors may have opted to publish only positive results. Yet negative results are real and reflect some ecological situations. In such cases where instability of the population becomes evident, we propose that production and productivity estimates both be calculated so as to present a broader picture including both realised and potential production estimates especially when gamete production can not easily be assessed.

Secondary production is a very sensitive property of populations. Small changes in mortality or growth patterns have a large impact on its assessment. Our results highlight the fact that population dynamics in a mussel bed, structured by an ice scouring events, can vary substantially from one level to another and lead to substantial variation in local net secondary production. Negative secondary production allows detecting rapid changes in populations, but we have also shown that production could be negative over a complete year of survey. There is definitely a need to produce more studies on local differences in production to detect patterns in local population dynamics and encourage comparison between different areas. Pooling of local (within population) mortality and growth data to reach a

global production estimate or calculation of productivity, should be avoided when assessing fine scale dynamics.

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FIGURE LEGENDS

Fig. 1. Study site at Pointe-Mitis (48º41'N; 68º02'W), Lower St. Lawrence Estuary (Québec, Canada).

Fig. 2. *Mytilus* spp. Seasonal abundance pattern in density (a, c, e, g, i; ind. m^{-2}) and tissue biomass (b,

5   d, f, h, j; g wet weight m^{-2}) for each age class (0 to >6 years old) for each sampling date (10 sample

dates for the sublittoral fringe level, 13 for the others) at Pointe-Mitis. Note the scale of the y-axis

varies among level.

Fig. 3. *Mytilus* spp. Monthly pattern of mean body mass (g wet weight, log scale with SE bars) by age

10   class (a, c, e, g) and monthly production (all age classes pooled; IS method; b, d, f, h) for all levels for

each sampling dates (10 sampling dates for the sublittoral fringe level, 13 for the others) at Pointe-

Mitis.

Fig. 4. *Mytilus* spp. Mean individual body mass (g wet weight, with SE bars) by age class for each

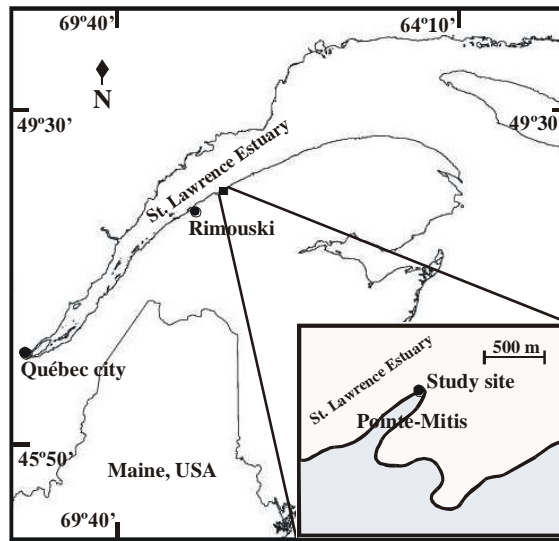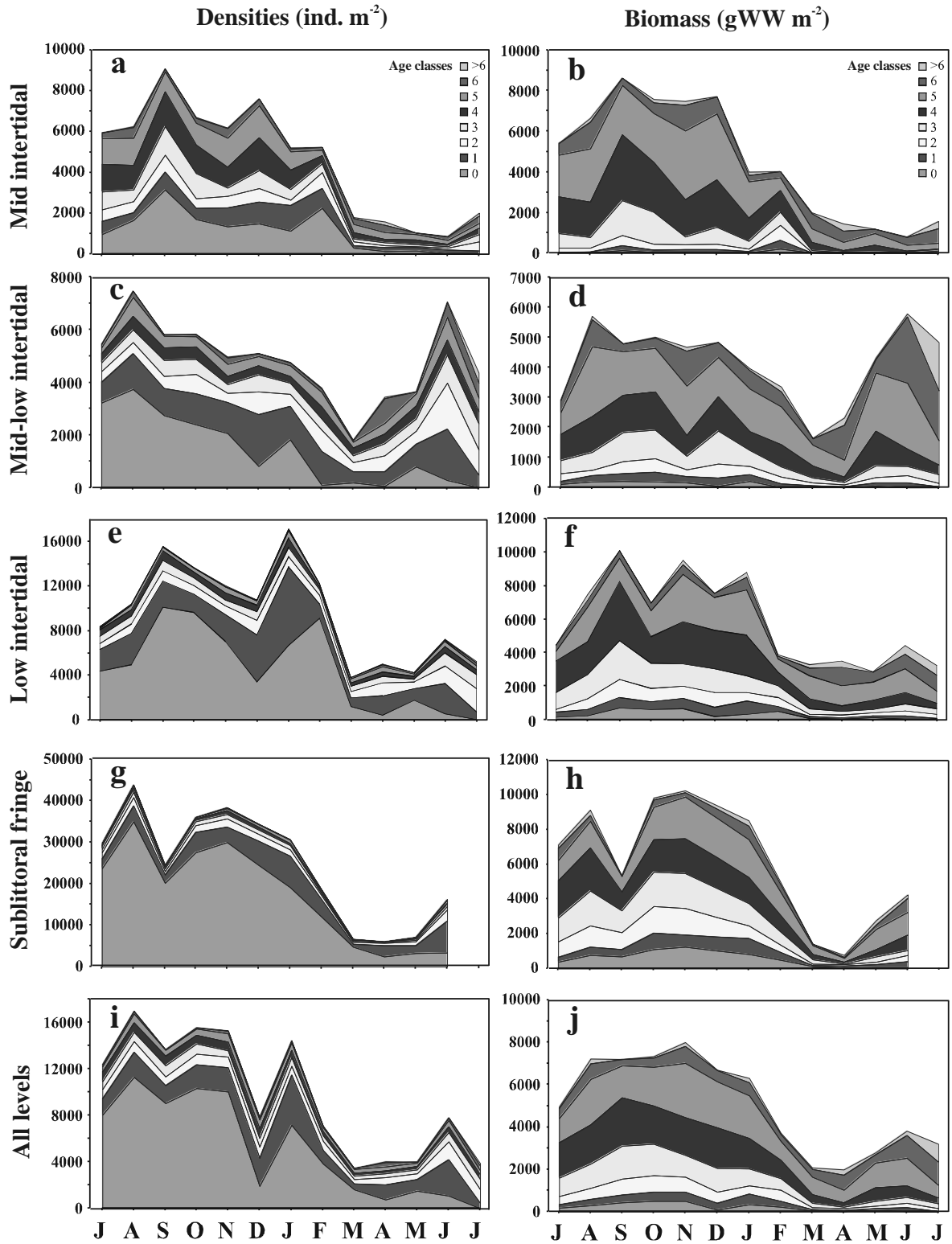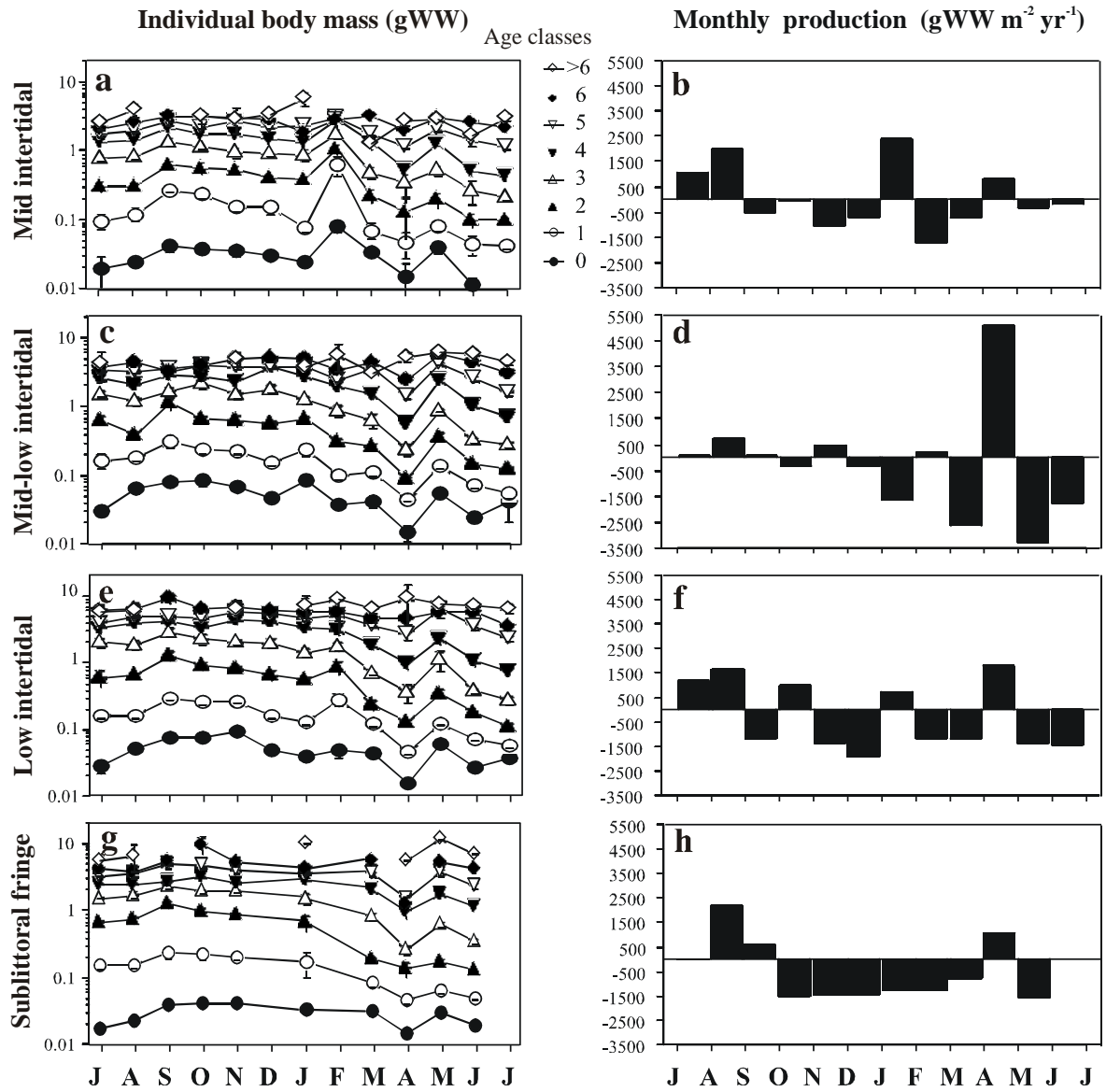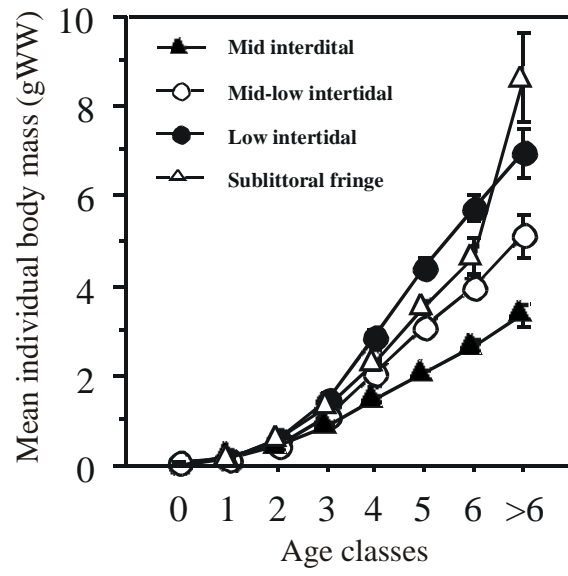15   level (all sampling dates combined) at Pointe-Mitis.

FIGURE 1

FIGURE 2

Densities (ind. m^{-2})   Biomass (gWW m^{-2})

FIGURE 3

Individual body mass (gWW)

Age classes

Monthly production (gWW m^{-2} yr^{-1})

FIGURE 4

5

Table 1. Annual *Mytilus* spp. production (g wet weight m^{-2} yr^{-1}), mean annual tissue biomass (gWW m^{-2}), mean annual density (ind. m^{-2}) and P/B ratio (yr^{-1}) from July 1979 to July 1980 for different shore levels at Pointe-Mitis. Increment summation production confidence intervals were assessed by bootstrap method (see text for details)

Levels	Annual production			Bootstrap confidence interval[a]			Mean annual biomass	Mean annual density	P/B ratio
	Increment summation	Removal summation	Elimination	Median	*p* (2.5)	*p* (97.5)			
Mid intertidal	923	922	5087	929	-1050	3078	5338	5416	0.17
Mid-low intertidal	-3325	-3325	-5104	-3490	-5166	-1544	4835	5676	-0.69
Low intertidal	-3276	-3276	-1985	-3252	-5865	-492	6565	10476	-0.50
Sublittoral fringe[b]	-2660	-2660	273	-2689	-4500	-936	5939	23932	-0.45

[a] Based on 1000 production calculation with the increment summation method using 10 quadrats randomly chosen with replacement
[b] from July 1979 to June 1980

Table 2. Some annual Mytilid growth production (kJ m^{-2} yr^{-1}) and P/B ratios (yr^{-1}) reported in the literature

Species	Study Area	Annual production	P/B ratio	Source
Choromytilus meridionalis	False Bay, South Africa			(Griffiths, 1981a)
	Topshore[*]	8396	0.45	
	Midshore[*]	11433	0.62	
	Lowshore[*]	15367	0.75	
	Sublittoral[*]	17694	0.98	
Modiolus demissus	Sapelo Island, Georgia, USA	58.2	0.27	(Kuenzler, 1961)
Musculista senhousia	Tomoe Cove, Amakusa, Japan	8.9-448	0.8-3.5	(Takana and Kikuchi, 1978)
Mytilus edulis/trossulus	Pointe-Mitis, Québec, Canada			This study
	Mid intertidal[†]	1130	0.17	
	Mid-low intertidal[†]	-4072	-0.69	
	Low intertidal[†]	-4013	-0.50	
	Sublittoral fringe[†+]	-3258	-0.45	
Mytilus edulis	Königshafen Bay, Germany	9969	0.36	(Asmus, 1987)
Mytilus edulis	Trinity Bay, NFLD Canada	11000	0.59	(Thompson, 1984)
Mytilus edulis	Delaware Bay, USA	0.4-305.4	1-6.2	(Howe et al., 1988)
Mytilus edulis	Slikken van Vianen, Netherland	4272	0.5	(Craeymeersch et al., 1986)
Mytilus edulis	Irish S., Morecambe B., GB	37030-66971	1.74-3.8	(Dare, 1976a)
Mytilus edulis	Quoddy Bay, N.-B., Canada	417.7	0.72	(Gardner and Thomas, 1987)
Mytilus galloprovincialis	Sacca di Scardovari, Italia	6940-12091	1.48	(Ceccherelli and Rossi, 1984)
Perna perna	Natal, South Africa	87907-90745	3.2-4.9	(Berry, 1978)
Perna perna	Gulf of Mexico, Texas, USA	40846-53853	1.25-1.38	(Hicks et al., 2001)
Perna picta	Temara, Morocco, Africa	16060	0.85	(Shafee, 1992)
Perna viridis	Tolo Harbour, H.-K., China	26190	0.28	(Cheung, 1993)

[*] mean of 3 years
[†] Using weight-to-weight and weight-to-energy ratio conversion factors: 0.05577 gAFDW/gWW; 21.96 kJ/gAFDW (cf Ricciardi and Bourget, 1998; Brey, 1999)
[+] from July 1979 to June 1980