



Padilla Bay

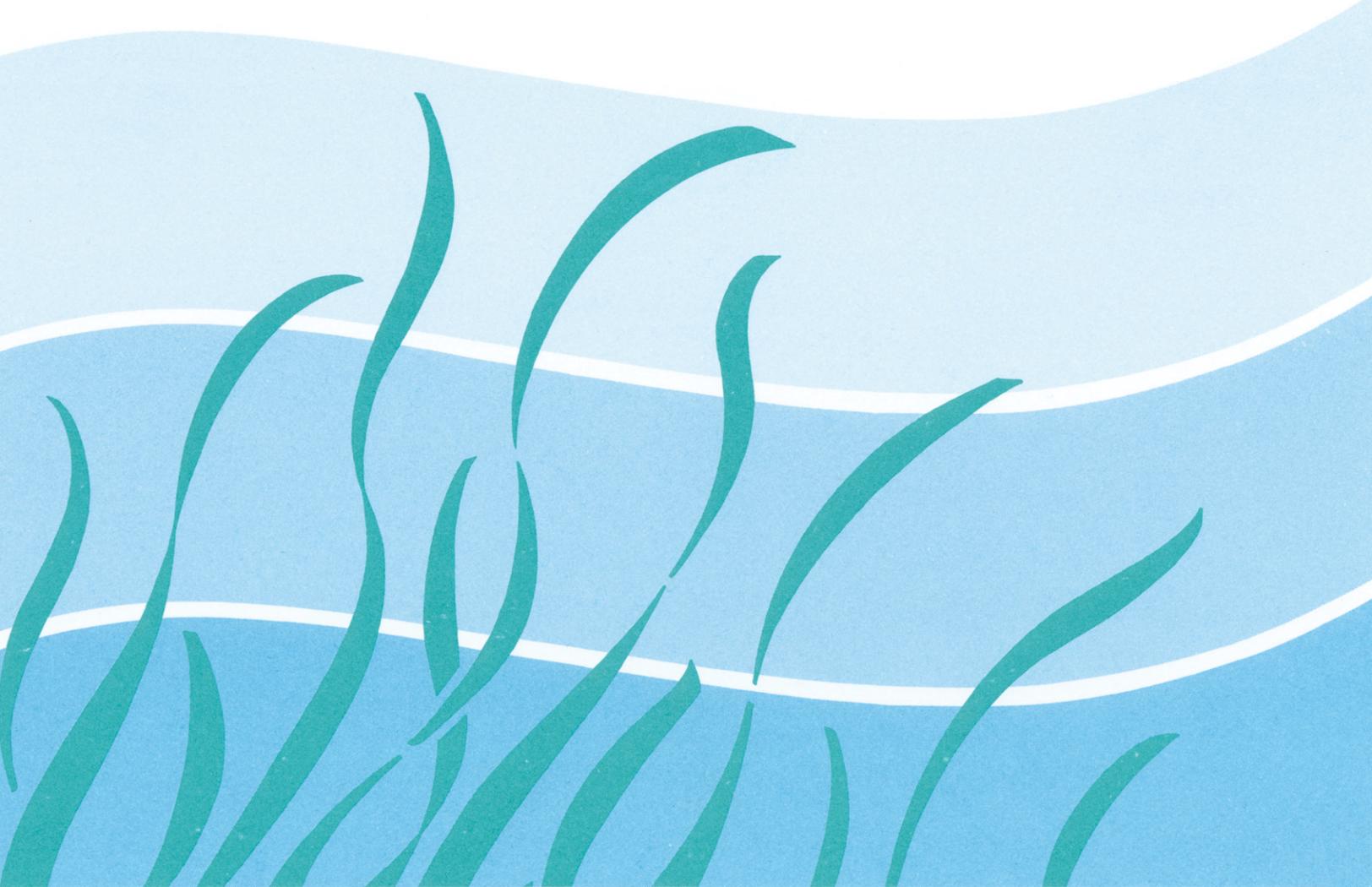
National Estuarine Research Reserve

Reprint Series No. 15
Reprinted April 1992

**TEMPORAL PATTERN OF GRAZERS AND VEGETATION
IN A TEMPERATE SEAGRASS SYSTEM**

R.M. Thom, B. Miller and M. Kennedy

1991



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TEMPORAL PATTERNS OF GRAZERS AND VEGETATION
IN A TEMPERATE SEAGRASS SYSTEM

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U.S. DEPARTMENT OF COMMERCE
NATIONAL OCEANOGRAPHIC AND ATMOSPHERIC ADMINISTRATION
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ABSTRACT

The density of grazers and the biomass of benthic vegetation were monitored for 10 months in the seagrass system in Padilla Bay, Washington. Experiments were conducted in the laboratory to evaluate the importance of grazing in the *Zostera marina* L. and *Zostera japonica* Aschers. & Graebn. subsystems in the Bay. The primary grazers included the isopod *Idotea ressecata*, the caprellid amphipod *Caprella laeviuscula*, the gastropod *Lacuna variegata*, black brant geese (*Branta bernicula*), and several species of dabbling ducks. Invertebrate herbivore density peaked in summer and autumn, in conjunction with peak plant biomass. The isopod probably removed more plant material than the other invertebrates. Spatial variation in grazing effect was substantial. Grazing pressure calculated from the experiments was always greater in the *Z. japonica* subsystem and exceeded a previous estimate of net annual primary productivity (NPP). The caprellids and isopods were prominent in the guts of shiner (*Cymatogaster aggregata*) and striped (*Embiotoca lateralis*) perch, two species commonly associated with seagrass systems in the Pacific Northwest. The presence of herbivorous birds, which are generally found in the system in autumn and winter, coincided with the period of most rapid loss of epiphyte biomass and eelgrass standing stock. However, birds appeared to remove less of the NPP as compared with invertebrates. We have concluded that herbivory is an important process in Padilla Bay in terms of controlling plant dynamics and may be a major pathway for the transfer of energy to higher trophic levels in this system.

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KEY WORDS

eelgrass, herbivory, seagrass system dynamics, seagrass system trophic structure

INTRODUCTION

Seagrasses form meadows that are ecologically complex and highly productive components of nearshore systems in subarctic through tropical latitudes (Phillips and Meñez 1988). In many instances, these meadows harbor a large number of fish and invertebrate species that depend upon the meadow for food and refuge. In some regions, commercially valuable fisheries resources are supported primarily by food produced in seagrass meadows (Stevenson 1988).

Although Pacific Northwest estuarine systems produce vast quantities of fisheries resources (Thom 1987), little is known about the production dynamics of the benthic plants or quantitative relationships between the plants and these resources. Eelgrass (*Zostera marina* L.) covers at least 25% of the coastline of Puget Sound, and occupies most of the low intertidal and shallow subtidal bottom in embayments (Thom and Hallum 1990). Although the productivity of these systems appears to be high (Thom 1990), and benthic productivity is important to nearshore food webs involving fisheries resources (Simenstad and Wissmar 1985, Ruckleshaus 1988), aspects of the dynamics of the pathways and fate of organic matter produced in eelgrass meadows are virtually unknown.

Previous studies have established that organic matter produced in seagrass systems is passed to higher trophic level via detritus (reviewed in Stevenson 1988). Another energetic pathway that has received somewhat less study in seagrass systems is grazing. Grazing has been shown to occur in seagrass systems, with types of grazers ranging from benthic crustacea such as isopods (Hootsmans and Vermaat 1985, Nienhuis and Groenendijk 1986), caprellid amphipods (Caine 1980), gastropods (Hootsmans and Vermaat 1985, Stoner 1989), sea turtles (Williams 1988), and birds such as brant geese (Nienhuis and Van Ierland 1978, Charman 1979, Jacobs et al. 1981). In addition, grazing of periphyton on seagrass can have an indirect influence on the dynamics and rates of seagrass productivity (Orth and Van Montfrans 1984, Hootsmans and Vermaat 1985). Finally, the stability of a system can be affected by grazing pressure; relatively high grazing pressure will destabilize the system (Noy-Meir 1975).

The purpose of the present study was to attempt to understand the role of herbivory as a pathway of organic matter from primary producers to consumers in a temperate eelgrass system in the Pacific Northwest. We hoped that by understanding herbivory we might be able to better quantify the role of eelgrass systems in nearshore food webs in the region. Preliminary data suggested that the isopod *Idotea ressecata* could graze a significant proportion of the plant production in the system we studied in Padilla Bay, Washington (S. Williams, Calif. St. Univ., San Diego, unpublished data). *Idotea* spp. are known to graze eelgrass and its epiphytes in the Netherlands (Hootsmans and Vermaat 1985, Nienhuis and Groenendijk 1986). Observations by Caine (1980) indicated that caprellids, which are dense at times in Padilla Bay, were important grazers in these types of systems. Birds which graze, including the black brant (*Branta bernicula*) and dabbling ducks, occur in the Bay in great numbers during autumn and winter (Phillips 1984). Herbivorous fish do not occur in the system, although some species such as shiner perch (*Cymatogaster aggregata*) are known to ingest epiphytes while feeding on invertebrates associated with periphyton on eelgrass leaves (Caine 1989).

Our study focused on invertebrate grazers, but we also conducted a limited evaluation of the impact of bird grazing. The objectives of the study were to: (1) quantify the seasonal changes in major invertebrate grazers; (2) couple these dynamics with seasonal changes in plant biomass; (3) estimate grazing rates of selected grazer taxa; and (4) provide an initial estimate of the amount of organic matter consumed annually by grazers. We relied on productivity data taken in 1986-87

(Thom 1990) for our estimate of net primary production in the system (ca., 28,000 mt dry wt). We know of no estimate of the effects of herbivory on productivity in Northwest benthic estuarine systems.

STUDY AREA

Padilla Bay is a shallow embayment in northern Puget Sound (Fig. 1). The tidal flats are dominated by eelgrass, which covers approximately 3,000 ha. Tides are mixed semi-diurnal with a mean range of 1.55 m. Salinity varies from 15 to 30‰. Water temperature in pools on the flats ranges from 7°C in December to 25°C in July (Thom 1990). *Zostera japonica*, a recent invader to the region, now occupies about 10% of the bay.

MATERIALS AND METHODS

STUDY SITES

We selected three study sites that spanned the depth gradient of eelgrass in the bay from the eight study sites used previously for productivity studies (Thom 1990). One of the sites (ZJ) was located in the *Z. japonica* subsystem at 0.6 m relative to mean lower low water (MLLW). The other two sites were located at 0.1 (ZM1) and -0.4 m (ZM4) MLLW within the *Z. marina* subsystem (Fig. 1). Each site consisted of a 20-m transect line positioned parallel to the edge of the water and marked at each end by wooden stakes. Sampling was carried out within sampling frames placed at random points along the transect line following the methods used previously (Thom 1990). Sampling points were located either 1 m shoreward or seaward from the line. Care was taken to avoid walking on, or otherwise disturbing, potential sampling points.

PLANT BIOMASS SAMPLING

A square frame enclosing 0.1 m² was used to sample *Z. marina*, and a circular frame enclosing 79 cm² (i.e., 10 cm diameter) was used for sampling the much smaller and more densely distributed *Z. japonica* shoots. All erect portions of the eelgrass shoots within the sampling frames were harvested at their base, placed carefully in labelled plastic bags, and frozen. Three replicate samples were collected at each site during each sampling trip. Sampling occurred in October, November, December 1989, and January, April, May and July 1990. Sampling was carried out during low tide. However, owing to the ponding that occurs on the flats, 5-30 cm of standing water covered the sites during samplings.

Frozen samples were thawed in the laboratory. The plants were placed in shallow trays containing tap water. Gentle rinsing removed most of the sediments associated with the plant material. Epiphytes, consisting of seaweeds (i.e., primarily *Enteromorpha* spp.) and filamentous and tube-dwelling diatoms were carefully scraped from five randomly selected shoots within each sample. The five shoots were dried to a constant weight in an oven at 80°C and individually weighed to the nearest mg. Epiphytes attached to the shoots were also dried and weighed. The total number of shoots in the sample was recorded. The total biomass of plants in the sample was determined by multiplying mean shoot weight by the number of shoots in the sample. Total epiphyte biomass was calculated similarly.

INVERTEBRATE GRAZER DENSITIES

The freezing and tap water rinsing separated virtually all of the macroscopic animals from the plant material so that the animals ended up on the bottom of the shallow pan. Animal taxa suspected of being grazers (i.e., caprellids, isopods, gastropods) associated with the plant material collected from the quadrats were enumerated, and the counts were converted to number of individuals per m². Grazer taxa identified in subsamples from the collections included the isopods *I. resecata*, *I. rufescens* and *Synidotea* sp., the gastropod *Lacuna variegata* (T. Nelson, Univ. Washington, Seattle, pers. comm.), and the caprellid *Caprella laeviuscula* (Caine 1980; Caine, Univ. Washington, Seattle, pers. comm.). *I. resecata* was by far the most abundant isopod taxon.

We also sampled grazer densities near the sites using a benthic sled sampler. The mouth of the sled was 20 cm high by 50 cm wide. A metal plate that spanned the width of the mouth was affixed to the bottom of the sled mouth and angled at approximately 45° toward the cod end. The net attached to the mouth was 250µm mesh size. The cod end was removable for access to material collected by the sled. Sled sampling was conducted at high tide within 24 hr of the low tide sampling. The sled was lowered to the bottom near the site, and towed for a distance of 20 m behind a small boat. We washed the material clinging to the net into the cod end prior to collecting the sample. The samples were placed into labeled plastic jars and preserved in buffered 5% formalin. Material was collected from three tows at each site. Floats placed at each end of the transects at each site were used to gauge the length of the tow and helped us avoid towing directly over areas where eelgrass samples would be taken. Animals collected in the first and second tows were identified to species and enumerated. The third tow was used to collect animals for the grazer experiments (see below). Densities per m² were calculated by dividing total counts in the tow by 10 m² (i.e., the area swept by the sled was 0.5 x 20 m = 10 m²). The results of the evaluation indicated that the sled was much less efficient in sampling the grazers as compared with the quadrat method. Densities estimated from the sled samples for *Idotea* were always lower than those from the quadrats and never exceeded 13% of the densities obtained from the quadrats. Hence, we used the quadrat samples for estimating densities and utilized the sled for gathering grazers for the experiments. We were able to obtain fresher samples using the sled because of the decreased transport time from the sites to an aerated cooler used for transporting the grazers to the laboratory.

INVERTEBRATE GRAZING EXPERIMENTS

We conducted several trial experiments to evaluate the feasibility of obtaining grazing rates on the three potentially most important grazer species in the system. These experiments consisted of placing grazers in 300-L aquaria with freshly collected eelgrass and observing animal behavior (i.e., the location of the animals, and the mode of feeding). Our observations indicated that *Idotea* was by far the most voracious of the grazers as evidenced by readily visible marks on leaves and by removal of epiphytes. Grazing of epiphytic algae by *Caprella*, although important when population densities are extremely high, was very difficult to observe and control on an individual or even at a controlled population (i.e., 20 individuals/tank) level owing to loss of individuals (i.e., escape or death). Individual grazing rates we felt would be very difficult to measure or estimate for this taxon. We therefore utilized *Idotea* for the experimental studies and relied on data from Caine (1980) for *Caprella* rates. Observations also indicated that *Lacuna* densities were generally low, and this species was probably much less important in the Padilla Bay system than in subtidal eelgrass systems in the Northwest (i.e., T. Nelson, Univ. Washington, Seattle, pers. comm.).

Animals and associated vegetation contained in the third tow at each site were transported to the laboratory in coolers containing seawater supplied with aeration from battery driven aquarium pumps. Experiments were conducted using cages made of polyvinyl chloride cylinders that were 10 cm in diameter and 10 cm long. Most of the sidewall of the cylinder was cut out and replaced with 250- μ m mesh screening to facilitate water flushing. One end, which formed the bottom of the cage, was covered with a lid made of mesh screening. The cages were placed in a water table (water depth = 8 cm) with flowing sea water. Ten-cm long strips of healthy portion of eelgrass leaves, were placed into each cage. Three leaf strips of the smaller *Z. japonica* were placed in each cage, and one leaf strip of *Z. marina* was placed in each of a set of different cages. Care was taken to place leaf sections that were of the same width, length, and approximate epiphyte biomass into each cage. Healthy, mobile, individuals of *Idotea* were placed into some cages. We selected individuals that were representative of size of the animals in the population collected. Control cages had only leaf sections. Observations were made every 1-3 days to evaluate whether measurable losses of leaf material were taking place. Experiments were stopped when grazing was obvious. Experiments were conducted at ambient sea temperature for varying lengths of time in October (3 days) and November (5 days) 1990, and January (16 days) and May (7 days) 1991. Four to 14 replicates were run for each treatment. We evaluated *Idotea* size range vs grazing rate during November and May experiments using 12 and 14 grazers, respectively. Measurements made at the end of the experiment included the length and dry weight of grazers, and the dry weight of leaf sections. The weight lost due to grazing was determined relative to the weight of leaf sections in the ungrazed controls.

BIRD GRAZING

We estimated grazing by birds from population counts for Padilla Bay supplied by the Washington State Department of Wildlife (M. Davidson, unpublished data) following the formula used by Nienhuis and Groenendijk (1986). Consumption (C) in gC m⁻² is calculated as follows:

$$C = \frac{(78.3 \times W^{.723} \times 0.2 \times 3 \times 1.67 \times 0.38 \times F \times BD)}{108 \times 10^6}$$

where $78.3 \times W^{.723}$ = converted body weight (W) to standard metabolism in kcal d⁻¹ (Lasiewski and Dawson 1967)

0.2 = converts kcal to g dry wt, and

0.38 = converts dry wt to gC (Westlake 1963).

Standard metabolism is multiplied by 3 to yield net food assimilation, and by 1.67 for food assimilation efficiency (Nienhuis and Groenendijk 1986). F is the fraction of the stomach contents comprised of benthic vegetation. We used F = 1 based on unpublished information from Padilla Bay (M. Davidson). The number of bird days (BD) was based on counts made during the fall and winter in 1989-1990 for dabbling ducks, including mallard (*Anas platyrhynchos*), northern pintail (*Anas acuta*), American wigeon (*Anas americana*), and green-winged teal (*Anas crecca*). Dabblers were counted on four occasions between October and December 1989, and brant were counted on six occasions between October and February. The average number of individuals based upon two consecutive observations was used as an estimate of the number of individuals observed each day of the period between the two consecutive observations. BD = average number of individuals x number of days between the observations.

FISH PREDATION

To evaluate the relative importance of grazers to the diet of fish in eelgrass food webs, we obtained lists of taxa found in the stomach contents of fish collected from seagrass meadows in the Pacific Northwest, including Padilla Bay (K. Li, Washington State Department of Fisheries [WDF]). The number of individuals of each fish species caught in the eelgrass beds was also provided. Sampling by WDF spanned from June to August 1989.

RESULTS

TEMPORAL DYNAMICS

Zostera japonica Site (ZJ)

Shoot density ranged from 2,164 to 5,093 m^{-2} during the study period. The standing stock of *Z. japonica* shoots was lowest in winter and greatest in mid-summer (Fig. 2A). Shoot standing stock was relatively low in October, indicating a major loss of biomass between mid-summer and autumn. Epiphytes followed this pattern, except that they reached their greatest mean biomass in autumn (Fig. 2B). Greatest *Idotea* density (Fig. 2C) occurred in summer in concordance with peak eelgrass standing stock and intermediate epiphyte biomass. *Lacuna* density (Fig. 2D) represented almost a mirror image of the *Idotea* density. Greatest densities of *Lacuna* occurred in autumn and winter. *Caprella* exhibited the most pronounced variations in the system, with low densities ($<100 \text{ m}^{-2}$) most of the year and a major peak in mid-July of over 20,000 individuals m^{-2} (Fig. 2E).

Zostera marina Site at 0.1 m MLLW (ZM1)

Shoot density varied between 260 and 600 m^{-2} . Shoot biomass and epiphyte biomass both peaked in autumn and were lowest in winter (Figs. 3A, B). *Idotea* and *Lacuna* densities at this site mimicked the pattern seen at the ZJ site (Figs. 3C, D). However, peak *Idotea* density was almost one-half that in the ZJ site. *Caprella* showed a peak in autumn-early winter and again in mid-summer (Fig. 3E) and never reached densities as high as that found in October at ZJ.

Zostera marina Site at -0.4 m MLLW (ZM4)

Eelgrass shoot density ranged between 170 and 290 m^{-2} , and biomass was generally stable throughout the year but showed a peak in mid-summer (Fig. 4A). ZM4 eelgrass biomass exhibited the least relative change in biomass among the three sites over the sampling period. Epiphyte biomass was also least temporally dynamic at this site (Fig. 4B), with small peaks indicated in November and July. Peak epiphyte biomass at ZM4 was about twice that at the other sites. In contrast with the other two sites, *Idotea* density peaked in mid-winter (Fig. 4C), and the peak mean value was approximately intermediate between peak values at the other sites. Similar to the other two sites, *Lacuna* showed a maximum that persisted between October and January (Fig. 4D). However, peak densities were ca. 600 and 1,000 individuals m^{-2} at ZM1 and ZJ, respectively, as compared with a peak mean density of ca. 150 individuals m^{-2} at ZM4. *Caprella* density exhibited

peaks in autumn and mid-summer (Fig. 4E) that were on the order of those seen at ZM1 but less than one-quarter of that measured in October at ZJ.

GRAZING

Invertebrates

Idotea consumed *Z. japonica* tissue, *Z. marina* tissue, and epiphytes attached to the plants. High variability prevented us from detecting difference in *Idotea* grazing rates between eelgrass species. In addition, epiphyte removal was generally 100% by the end of the experiments, and graze marks were evident in leaves. Therefore, we chose to combine data from both eelgrass species, and we lumped epiphyte biomass with leaf tissue biomass in the calculation of grazing rates. Fecal pellets were common at the bottom of the cages where grazing was heaviest.

Idotea mean grazing rate for all experiments was 0.954 mg dry wt. individual⁻¹ day⁻¹ (n = 36, SE = 0.188). Mean dry weight and length of animals used in the experiments were 28.132 mg (n = 41; SE = 5.059) and 18.1 mm (n = 41; SE = 1.5), respectively. Grazing rate varied by animal size and season, with the intermediate sized animals collected in November having the greatest grazing rate per individual (Fig. 5). The greatest ratio of grazing rate to weight per individual *Idotea* (0.17 and 0.16, respectively) were shown in November and January. Ratios for October (0.02) and May (0.01) were much lower.

The temporal trend in grazing by *Idotea* in the ZJ and ZM (i.e., ZM1 and ZM4 data averaged) indicated that grazing pressure varied with season and site (Fig. 6). Grazing was greater in ZJ than ZM during all months, with maxima in November and summer (June–August). Similar trends were apparent in ZM, although there was a peak in December instead of October.

Net annual primary productivity (NPP) by *Z. japonica* and associated epiphytes estimated in 1986–7 (Thom 1990) was 66 gC m⁻². If the monthly grazing rates are summed, the total amount grazed in the ZJ subsystem was 649 g dry wt y⁻¹. This converts to 246 gC m⁻² yr⁻¹ using a carbon to dry weight ratio of 0.38 (Westlake 1963). Hence, *Idotea* grazing greatly exceeded (i.e., 2.6 times) the estimated annual NPP of the eelgrass and algae at this site (Table 1). For the ZM subsystem, NPP was estimated in 1986–87 to be 405 gC m⁻² y⁻¹ (Thom 1990). *Idotea* grazed a total of 38 gC m⁻² during the year or about 9.4% of net primary productivity (Table 1).

There were more *Idotea* per shoot at ZM4 as compared with the other two sites except during July (Fig. 7). The number of individuals per shoot ranged from ca. 0.5 to 7. The number of *Lacuna* per shoot was always less than two and was generally much less than one at all sites. Maximum mean number of *Caprella* per shoot was 16. However, *Caprella* densities per shoot were generally less than two.

Observations made in the aquaria indicated that *Idotea* readily ate epiphytes and eelgrass leaves. The isopods were extremely motile, swimming actively between shoots. *Caprella* and *Lacuna* were observed to scrape the surface of the leaves for epiphytes and other attached organisms. These latter taxa were much less motile than the isopods and generally remained attached to the same leaf, with very little movement, during the period of observation (generally 0.5 h). We observed that live and standing dead (i.e., light brown in color) leaf material was consumed in the aquaria and in the cages by *Idotea*. We were unable to determine if the other taxa were also consuming dead leaf tissue.

Bird Grazing

Dabbler and brant abundance peaked in December and February, respectively (Fig. 7). On December 7, bird grazer total abundance exceeded 100,000 individuals. This peak corresponds with low points for eelgrass and epiphyte biomass at all sites. Collectively the birds consumed $5.253 \text{ gC m}^{-2} \text{ y}^{-1}$, which was 1.5% of the total annual NPP for the eelgrass system (ZJ and ZM weighted average based upon area covered = $351 \text{ gC m}^{-2} \text{ y}^{-1}$; Thom 1990). Dabblers ate 1.12% and brant ate 0.38% of the total annual NPP. Because no data are available on birds after February, C is underestimated for the system. However, the majority of waterfowl leave Padilla Bay by March (M. Davidson, Washington State Dep. Wildlife, Olympia, WA, pers. comm.).

FISH PREDATION

The information on diets of fish indicated that striped perch (*Embiotoca lateralis*) and shiner perch were found in relatively high densities in eelgrass meadows in the Pacific Northwest and were preying primarily on amphipods, caprellids and isopods (K. Li, Washington State Dep. Fisheries, unpublished data). *I. resecata* was prominent in the guts of striped perch and *C. laeviuscula* was prominent in all embiotocids.

DISCUSSION

The densities of grazing invertebrates varied in space and time in the Padilla Bay eelgrass system. Although complex, the general pattern in Padilla Bay showed a pronounced peak in invertebrate grazer densities in mid-summer, and a more prolonged increase in autumn and winter. The summer peak coincided with periods of intermediate to maximum biomass of eelgrass and its epiphytes. The autumn-winter high densities, which included large populations of overwintering waterfowl, coincided with the period of most rapid loss of plant biomass that had built up through rapid growth during spring and summer.

Grazing is an important process in Padilla Bay. Mean annual NPP for the eelgrass system (eelgrass plus epiphytes) is 351 gC m^{-2} (Thom 1990). This amounts to a total of $10.5 \times 10^6 \text{ kgC}$ for the entire bay. *Idotea* consumed 246 and 38 gC m^{-2} in the *Z. japonica* and *Z. marina* subsystems, respectively. Birds consumed 5.3 gC m^{-2} . Extrapolating these values to the total system produces a total consumption of $2.3 \times 10^3 \text{ kgC yr}^{-1}$ or 22% of the annual NPP in the bay. Grazers also may be important contributors to the degradation process that occurs in autumn and winter in the system.

Plant biomass and productivity exhibit dynamic seasonal patterns in Pacific Northwest estuarine systems (Thom 1987, Thom and Albright 1990). The initiation of the spring increase appears to be controlled by light increases, and the cessation of growth is in response to decreased light and other factors. However, the factors that regulate the total biomass during the periods when light is not limiting photosynthesis are not well known. The present data suggest that grazers may regulate plant biomass accumulation during productive periods and interact significantly in degradative processes that occur after the productive period. On the basis of the numbers of individuals per eelgrass shoot, grazing rates, and total percentage of annual NPP grazed (9.4%), we conclude that *Idotea* can have a significant effect on biomass accumulation in the system. In separate studies, *Idotea chelipes* consumed 3.8% (Nienhuis and Groenendijk 1986) and 5.0% (Nienhuis and Van Ierland 1978) of the annual NPP in Lake Grevelingen, a marine lagoon in southwest Netherlands.

Grazing pressure appeared to be greatest at the *Z. japonica* site. We estimated that *Idotea* alone could remove much more (i.e., 2.6 times the annual NPP) biomass than is produced at the *Z. japonica* site. Inclusion of the other grazers would increase the amount of biomass consumed. Isopod densities of 1,000-7,000 individuals m^{-2} are high compared with studies conducted in Lake Grevelingen, where maximum mean densities of *I. chelipes* were ca. 1,200 m^{-2} (Nienhuis and Groenendijk 1986). Even though the number of individuals per shoot was relatively low at the ZJ study site compared with ZM1 and ZM4, the leaf area (maximum leaf size ca. 15 cm long x 0.2 cm wide) was much smaller than for *Z. marina* (maximum leaf size at ZM4 ca. 200 cm long x 1 cm wide). Our data on interpolated grazing rates in the *Z. japonica* and *Z. marina* subsystems indicated that grazing pressure was always higher in the *Z. japonica* subsystem. These results indicate that *Z. japonica* is a significant contributor to the food web through the grazer component in Padilla Bay, and that grazers may play a major role in the highly dynamic temporal patterns of biomass for this species. Interestingly, this species has recently invaded Pacific Northwest systems and appears to have taken on an important role within the systems.

Grazing at the *Z. marina* sites is probably important in controlling biomass accumulation in spring and summer and biomass loss in autumn. Daily epiphyte productivity rate is very high and exceeds *Z. marina* productivity in spring in Padilla Bay (Thom 1990). In summer, epiphyte productivity falls to a low level. *Idotea* and *Caprella* reach high densities in summer, perhaps shortly following the period of highest epiphyte production. The relatively low epiphyte biomass in July at ZM1 may be due to the increased grazing by these animals. The increase in *Lacuna* and *Caprella* densities in autumn and winter corresponded with the decrease in epiphyte biomass. The fact that the numbers of *Lacuna* per shoot were very low (<1) suggests that these small animals (ca. 2- to 4-mm shell height) had little effect on the decline of epiphytes (or eelgrass) biomass in the autumn. We have noted *Lacuna* densities on the order of 50-200 individuals on single shoots of eelgrass in subtidal meadows. In such cases, the leaves are devoid of epiphytes. *Caprella* may have had a major role in biomass degradation during the period when their densities per shoot were relatively high. Caine (1980) found that eelgrass epiphyte biomass was 411% greater in aquaria without *Caprella* as compared to aquaria stocked with *Caprella* at a density of 177 individuals shoot⁻¹. He found that protected eelgrass beds contained *Caprella* densities of 44.2 individuals shoot⁻¹. Mean caprellid densities we measured were always less than 7 individuals shoot⁻¹ at ZM1. Although *Caprella* reached densities of 16 individuals shoot⁻¹ at ZM4, densities were generally below 3.

It is difficult to reasonably manipulate grazer densities in the eelgrass system we studied, which is why we relied on experiments conducted under highly artificial conditions in aquaria. Several factors must be considered when viewing grazing rates for animals in cages placed in aquaria, especially highly motile species. First, *Idotea* was noted to swim at very rapid rates in the field. Swimming utilizes significant amounts of energy, and this same expenditure was not simulated in cages. Our experiments verified that the invertebrate species we focused on were grazers, but rates in the cages may underestimate what occurs in the field. Second, the grazers may undergo mass movements on a diel basis, and samples collected at low tide at the sites may not be indicative of the densities at higher tides. Simenstad et al. (1988) showed that epibenthic harpacticoid copepods, which are probably not as highly motile as *Idotea*, do exhibit distributional changes with the tide in Padilla Bay. Our sampling with a sled at high tides did indicate that grazer densities were different between the sites. However, because the sled was inefficient in collecting grazers, we cannot say conclusively whether spatial patterns seen at low tides were representative of patterns at all stages of the tide. Finally, the architecture of the leaves and bed (e.g., leaf length and shoot

density) affects animal abundances (Stoner 1980). These factors are not simulated in aquaria. Data on spatial patterns of grazers over the diel cycle is required to fully understand the grazing pressure in the system.

Birds consumed a small percentage (1.5%) of the annual NPP. With a peak abundance of ca. 100,000 individuals, bird density was on the order of ca. 33 individuals ha⁻¹ of eelgrass. This value is about twice as high as that recorded in the 4,000-ha eelgrass meadow in Lake Grevelingen (S.W. Netherlands, Nienhuis and Groenendijk 1986). Consumption by birds, which has been studied extensively in that system, was estimated to be on the order of 3.7% of annual NPP (Nienhuis and Groenendijk 1986, Nienhuis and Van Ireland 1978). The data from Lake Grevelingen includes bird counts throughout the year. Bird counts for Padilla Bay were available for only a part of the year, which may account for the reduced estimate of grazing. However, eelgrass NPP for Lake Grevelingen was estimated to be ~35 gC m⁻² yr⁻¹ compared with ~200 gC m⁻² yr⁻¹ for Padilla Bay (Thom 1990). Hence, birds may exhibit a greater relative influence on the eelgrass in Lake Grevelingen because of the much lower annual NPP.

There are limited observations (T. Stevens, National Estuarine Research Reserve, Padilla Bay, pers. comm.; K. Brunner, Seattle District, U.S. Army Corps of Engineers, pers. comm.) indicating that dabbling ducks feed on *Z. japonica*. We did note that most leaves of *Z. japonica* were broken at the tips during late summer through winter, which may be due to bird foraging. *Zostera japonica* could serve as an important resource for grazing birds in the Padilla Bay system.

The interaction between removal of epiphytes and increased production of eelgrass (Sand-Jensen 1977, Orth and Van Montfrans 1984) was not studied by us but also may be important in the system. Epiphyte load can exceed the biomass of eelgrass during spring and early summer in seagrass systems (e.g., Penhale 1977); this has been shown to occur in Padilla Bay (Thom 1990). At this level, growth of eelgrass due to light inhibition by the epiphytes and perhaps competition for inorganic nutrients would surely be affected. Unpublished data from Padilla Bay (S. Williams, Calif. State Univ., San Diego) indicated that grazing of epiphytes by *Idotea* ameliorated the positive effect of increased water column nutrients on epiphyte growth (and subsequent reduction in eelgrass growth). We have noted that during studies conducted in the bay since 1986 the epiphyte loads varied annually. Seaweeds were noted to bloom extensively in areas of eelgrass (and perhaps grazers) killed by a severe winter freeze in 1988–89. There is also an indication that *Z. marina* annual NPP is greatest where epiphyte NPP was lowest in Padilla Bay (Thom 1990).

According to the definitions and models presented by Noy-Meir (1975), the *Z. japonica* subsystem is unstable and the *Z. marina* subsystem is stable. Grazing exceeds vegetation growth in the former subsystem, which will lead to plant extinction if there is no plant reserve capable of providing new growth. *Zostera japonica* reproduces by seed annually. Although seed production has not been documented for the bay, studies by Nomme (1989) on Roberts bank (ca. 30 km north of Padilla Bay) indicate that seed density can be very high in sediments in that bed, and that seed viability is also very high for this species. An annual high rate of seed production may be how *Z. japonica* "escapes" extinction. In general, annual plants that occupy vacant ground space (i.e. ruderals) regenerate annually by seeds (Grime 1979). In contrast, perennials such as *Z. marina* regenerate via vegetative growth. Flowering by *Z. marina* is generally low (i.e., less than 10% of the shoots produce flowers in Padilla Bay). However, variations in annual climatic processes such as freezes and inputs of fertilizers and pesticides from surrounding agricultural lands may affect the biomass of eelgrass, epiphytes, and grazer densities, which would tend to destabilize the subsystem. The quantification of these linkages would be necessary to adequately model system stability.

The grazers are an important part of the diet of fish in eelgrass systems in the Northwest, which indicates that grazers are an important link between benthic plants and higher trophic levels. Shiner and striped perch are known to prey heavily on *Idotea* and *Caprella* (Caine 1989) in Padilla Bay. These fish species can reach very high densities (9 individuals m^{-2}) in eelgrass meadows in northern Puget Sound in mid-late summer (Thom et al. 1989). The interaction of predation on grazers by fish in the system is undoubtedly significant, but the degree to which fish predation regulates grazer densities is unstudied in Pacific Northwest systems.

Considerable differences were apparent in the seagrass system based upon samplings of the same sites in 1986–1987 (Thom 1990) and 1989–1990. Eelgrass biomass at ZM1 and ZM4 was lower in 1989–1990 as compared with 1986–1987 (Thom 1990). For example, the biomass in May at ZM1 and ZM4 during 1987 was ca. 125 and 285 g dry wt m^{-2} , respectively. This compares with 1990 values of ca. 22 and 60 g dry wt m^{-2} for ZM1 and ZM4, respectively. Epiphyte biomass was also much greater in May in 1986 (ca. 30 g dry wt m^{-2}) and 1987 as compared with 1990 (ca. 1 g dry wt m^{-2}). These data suggest that either benthic primary productivity was greater or grazing pressure was less in 1986–1987. We did note (qualitative observations) a general decline in eelgrass abundance in Pacific Northwest estuaries in 1988–1989 due to unusually long periods of freezing, which corresponded with extreme low tides in December and January of 1988 and 1989. Sites at Padilla Bay observed in the summer of 1989 had substantially less eelgrass cover and an unusually high abundance of ephemeral seaweeds (e.g., *Enteromorpha prolifera*, filamentous diatoms), which occupied space formerly held by *Zostera*. Only quantitative, long-term monitoring can verify the interaction between plant fluctuations, grazers, and stochastic events.

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Figure 1. Padilla Bay showing the sampling sites.

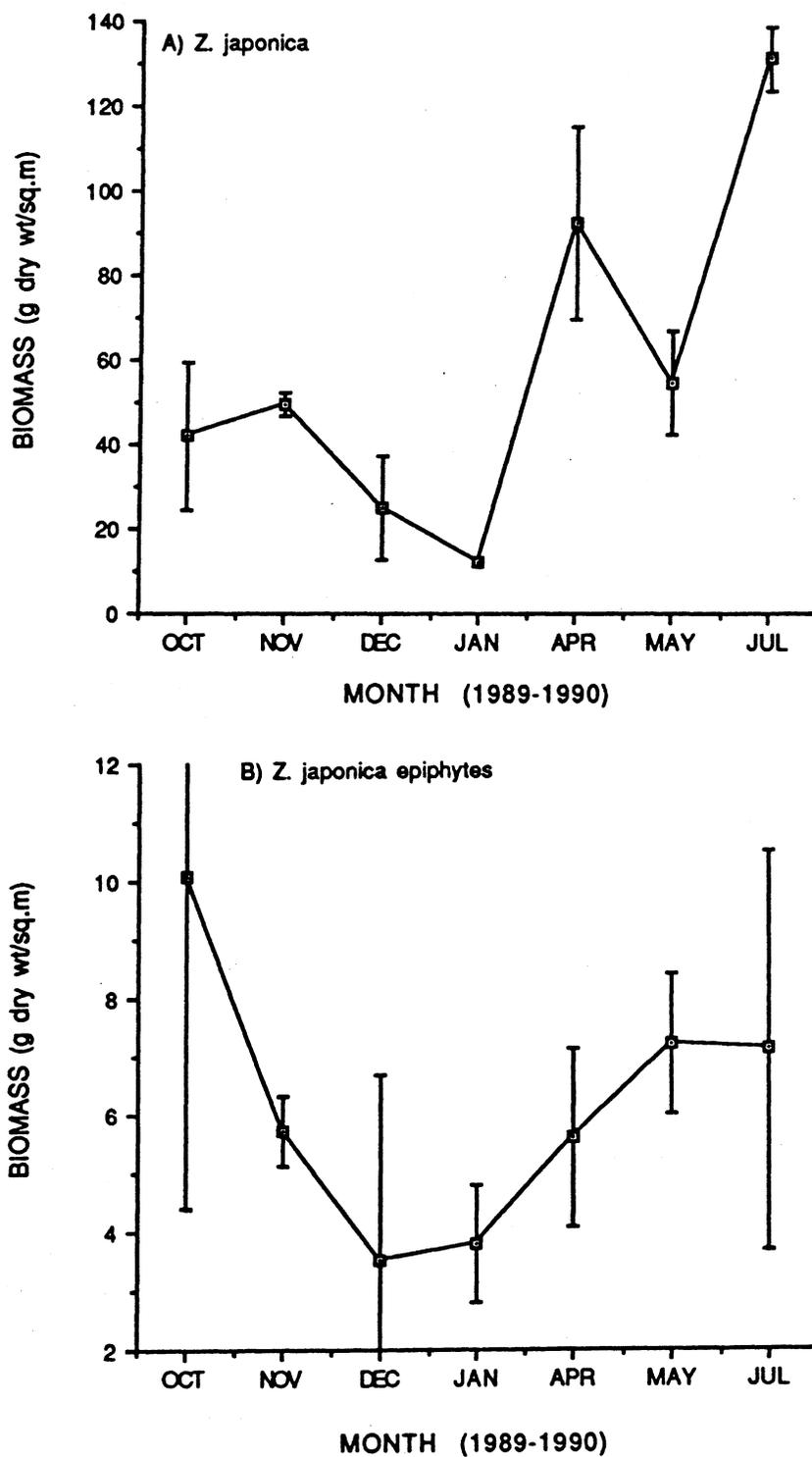


Figure 2. Temporal variations of mean (\pm SE) of vegetation and grazer parameters at the *Zostera japonica* site: (A) *Z. japonica* biomass; (B) epiphyte biomass; (C) *Idotea* density; (D) *Lacuna* density; (E) caprellid density.

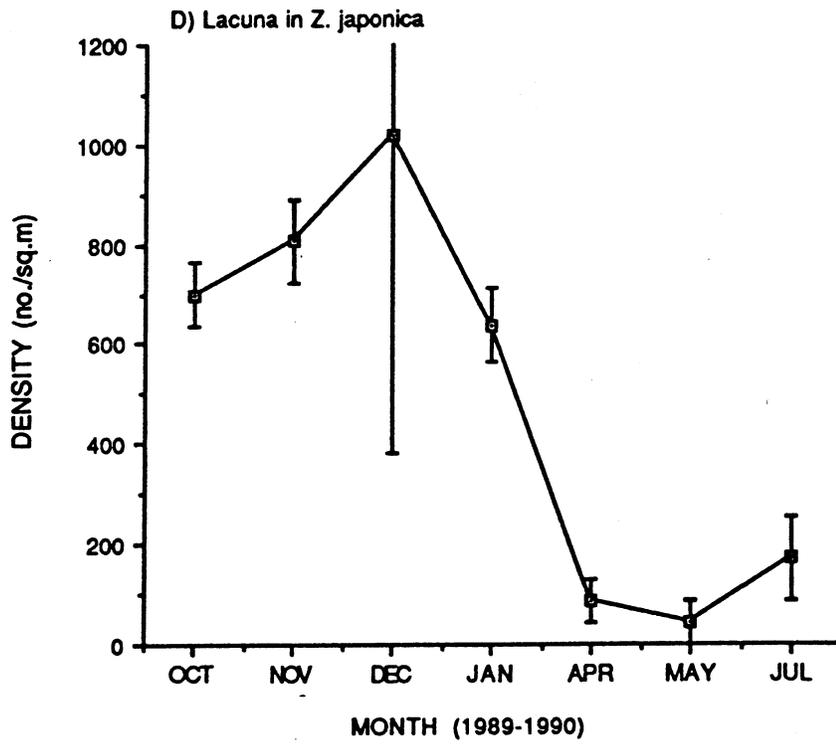
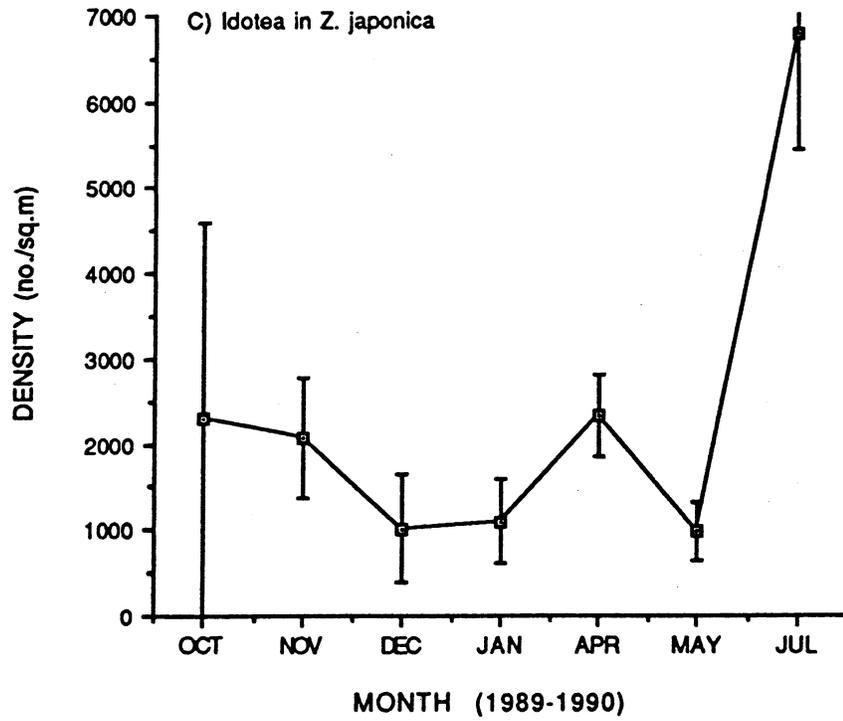


Fig. 2—cont.

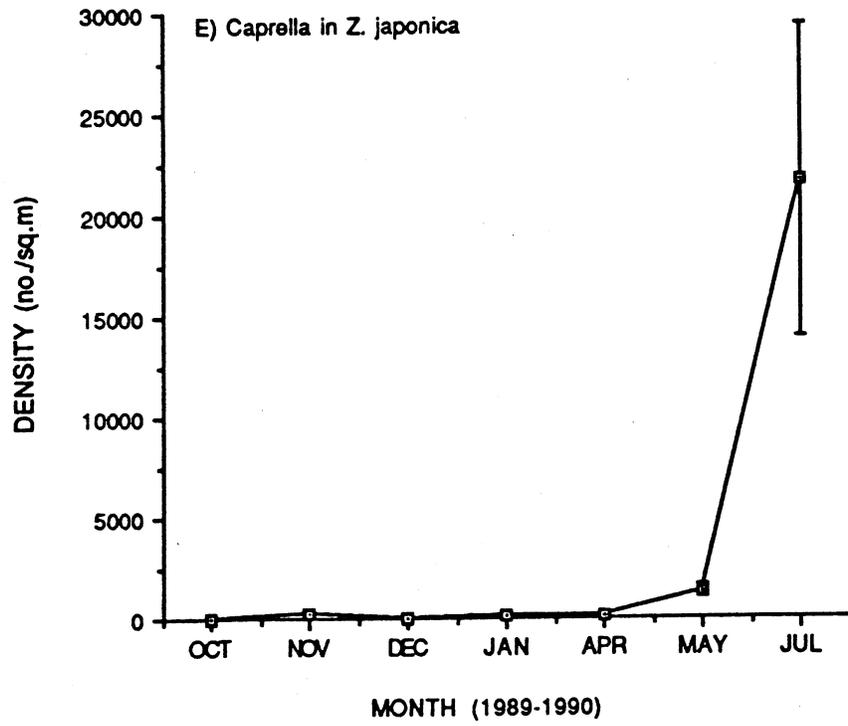


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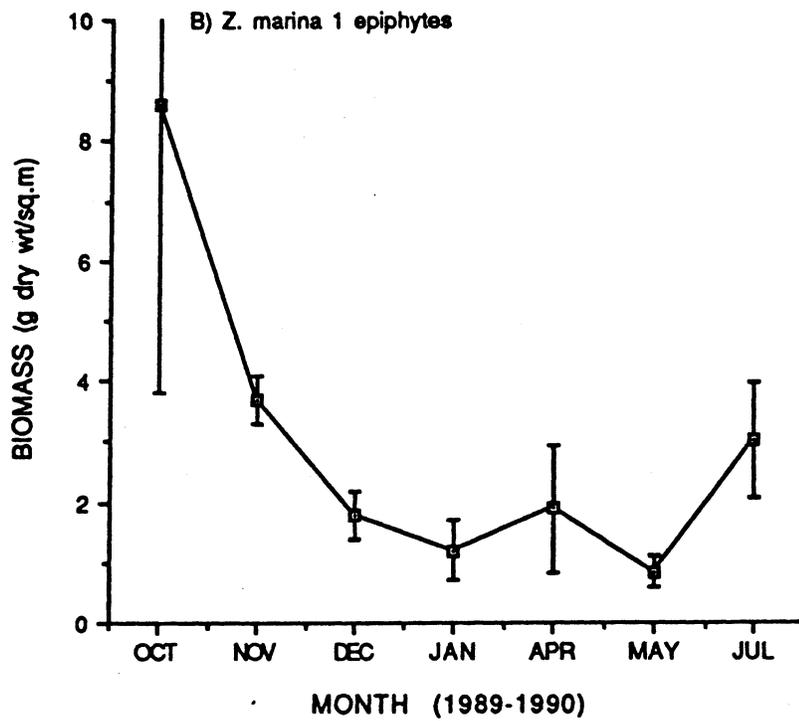
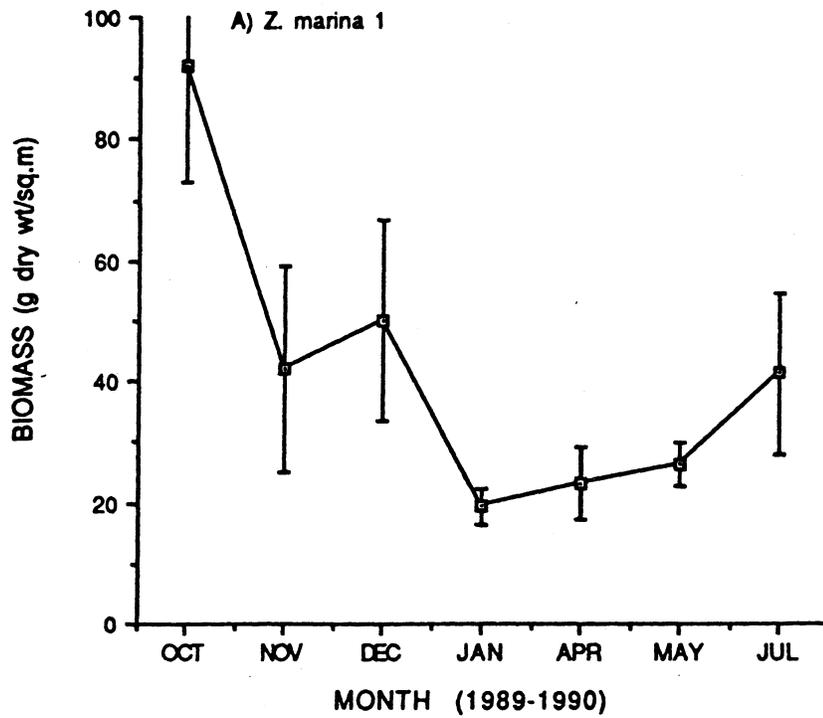


Figure 3. Temporal variations of mean (\pm SE) of vegetation and grazer parameters at the *Zostera marina* 1 site: (A) *Z. japonica* biomass; (B) epiphyte biomass; (C) *Idotea* density; (D) *Lacuna* density; (E) caprellid density.

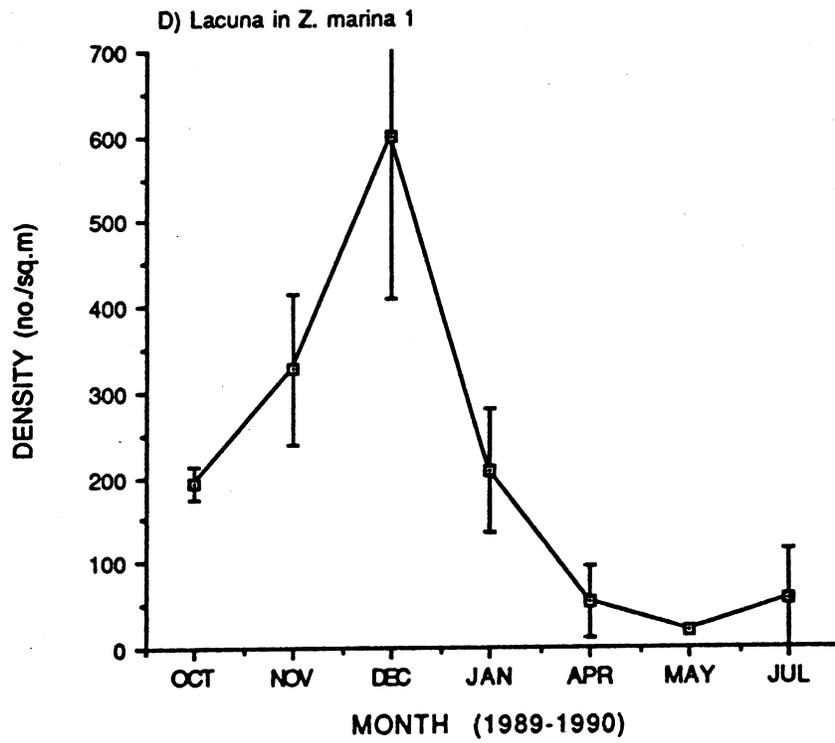
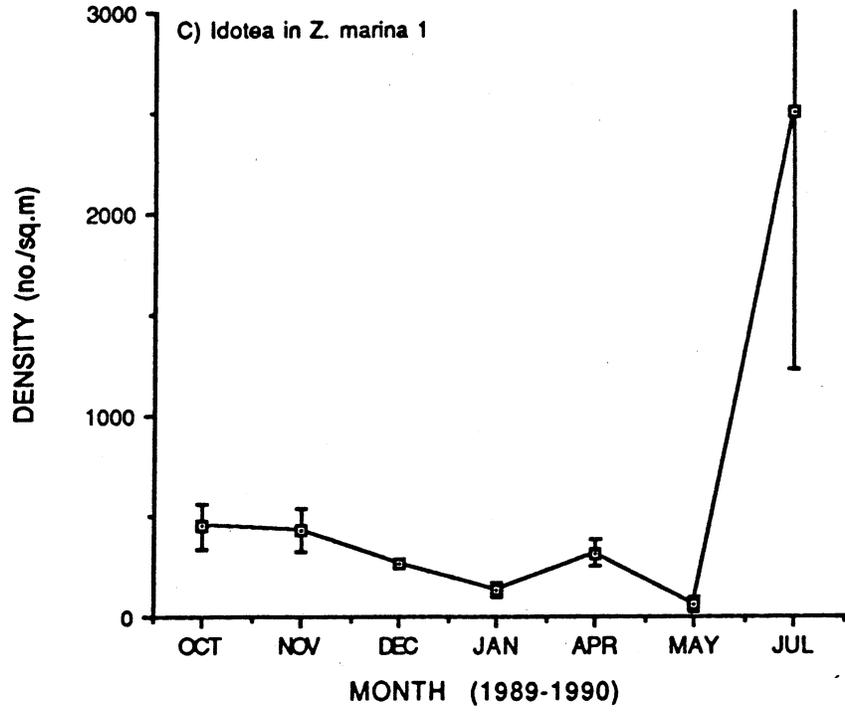


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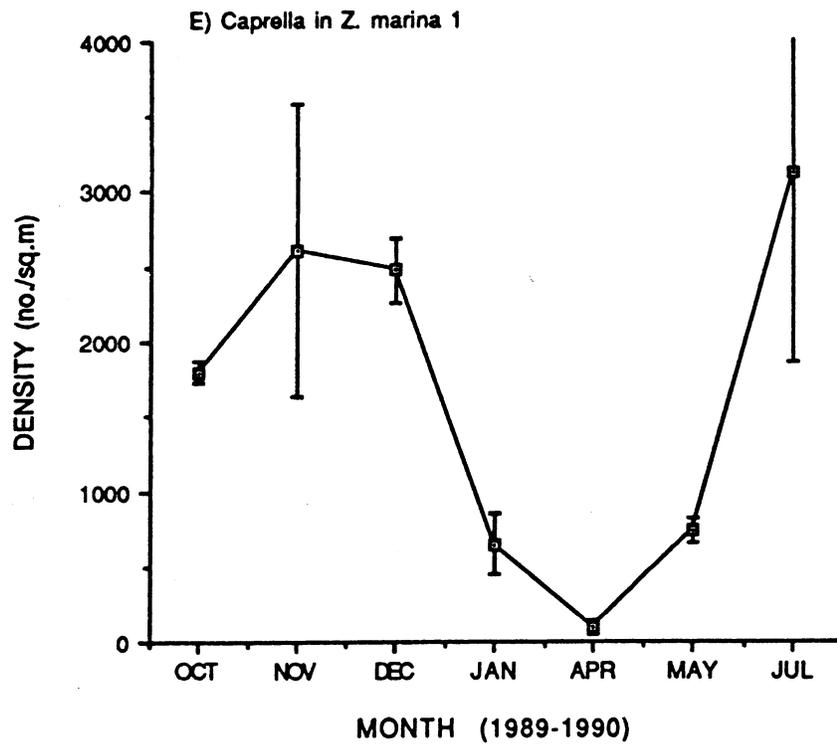


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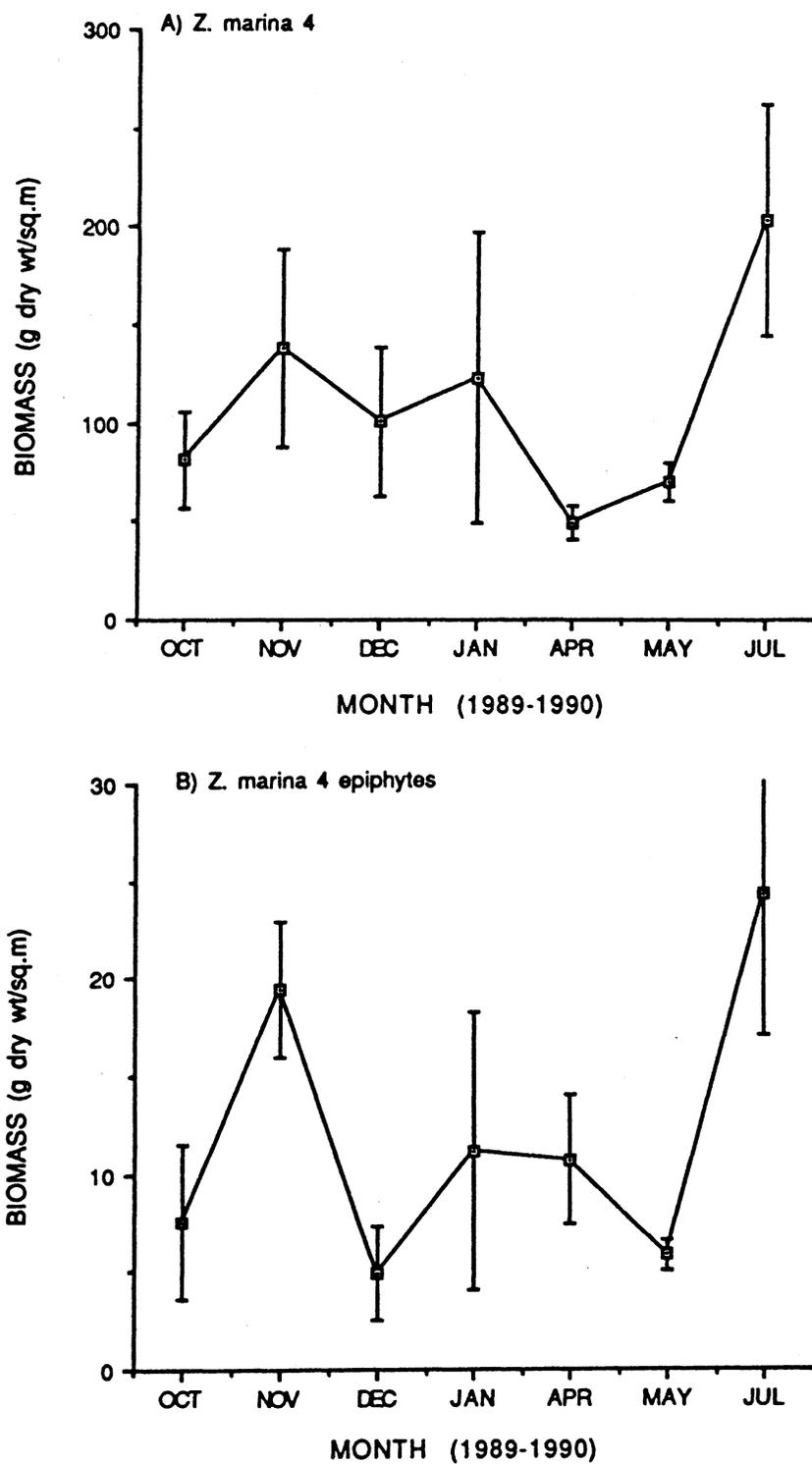


Figure 4. Temporal variations of mean (\pm SE) of vegetation and grazer parameters at the *Zostera marina* 4 site: (A) *Z. japonica* biomass; (B) epiphyte biomass; (C) *Idotea* density; (D) *Lacuna* density; (E) caprellid density.

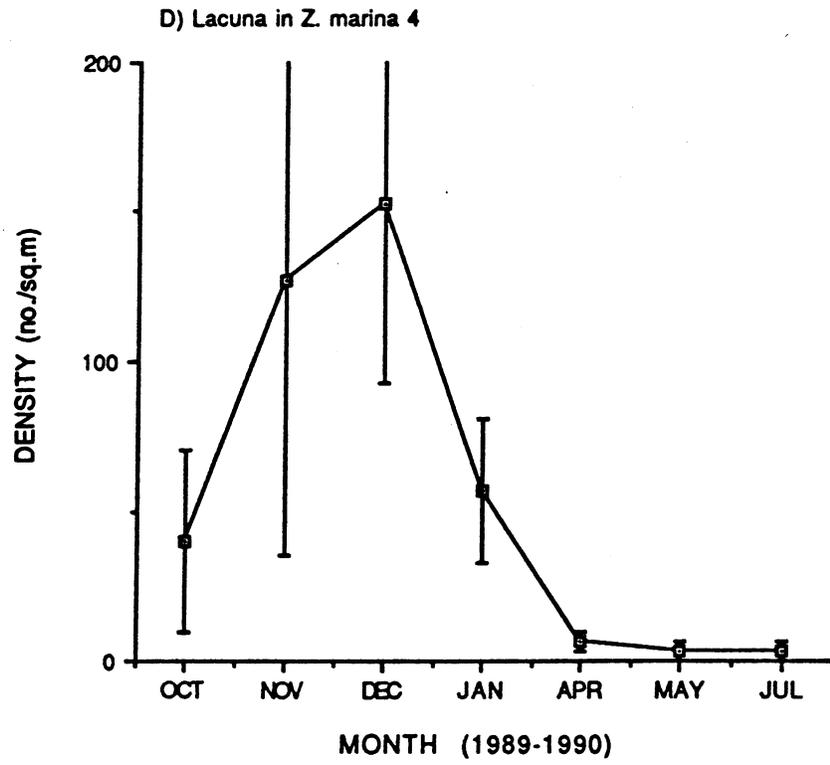
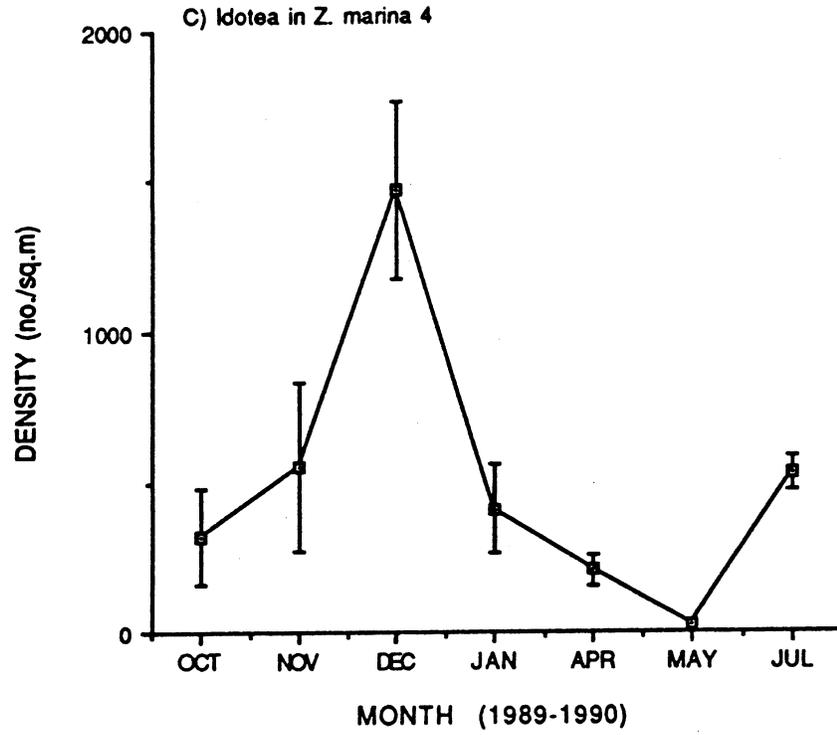


Figure 4—cont.

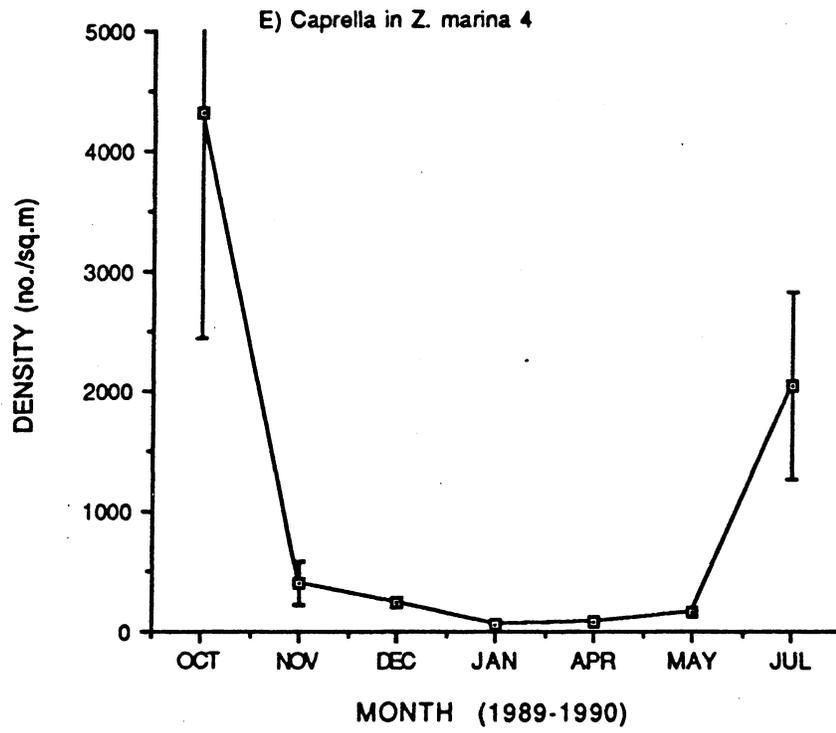


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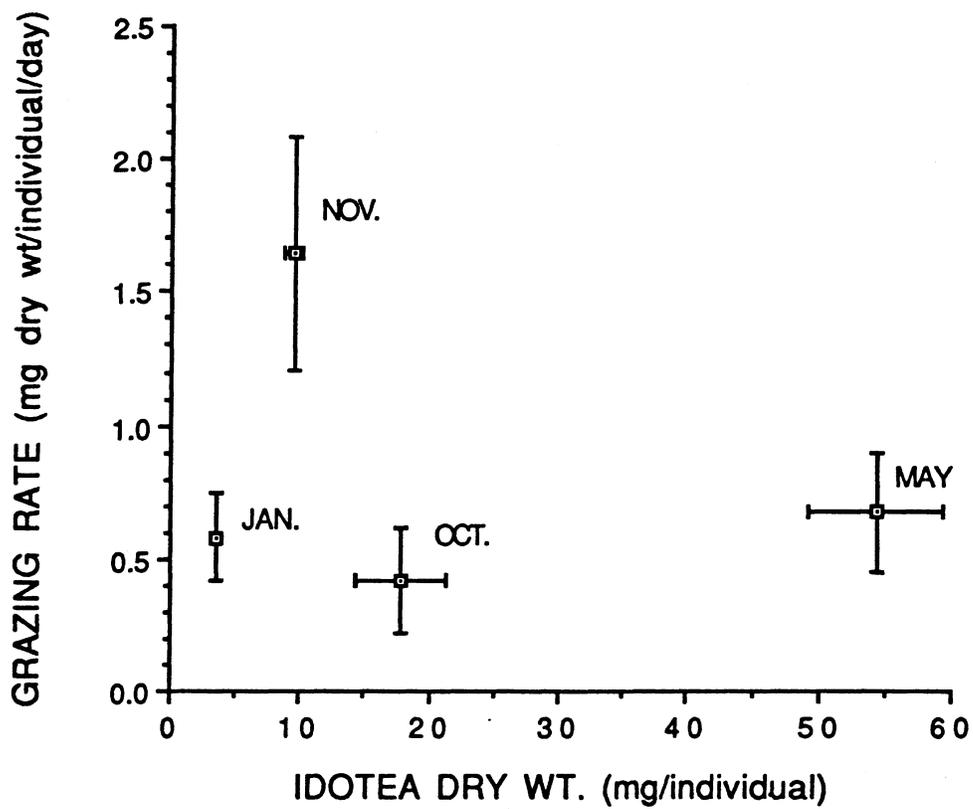


Figure 5. Mean (\pm SE) *Idotea* grazing rate based upon laboratory experiments.

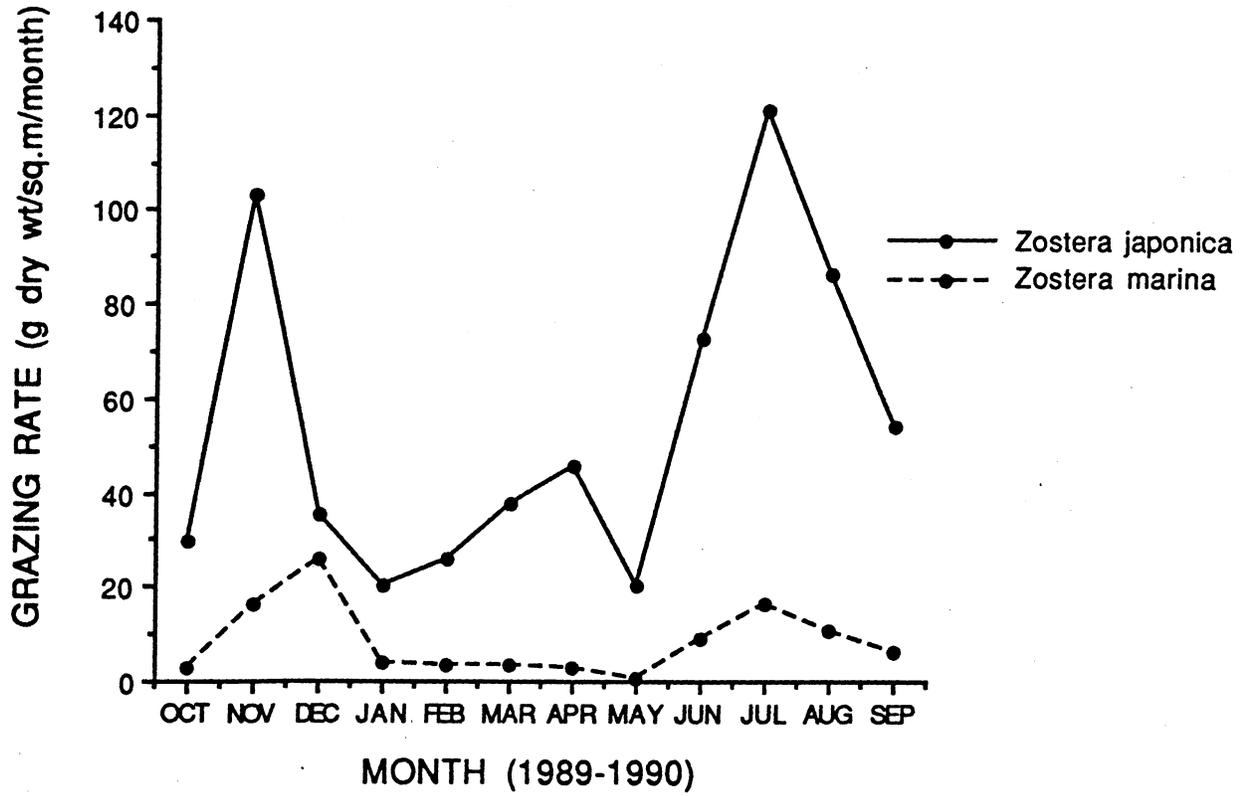


Figure 6. Grazing rate of *Idotea* in *Zostera japonica* and *Zostera marina*.

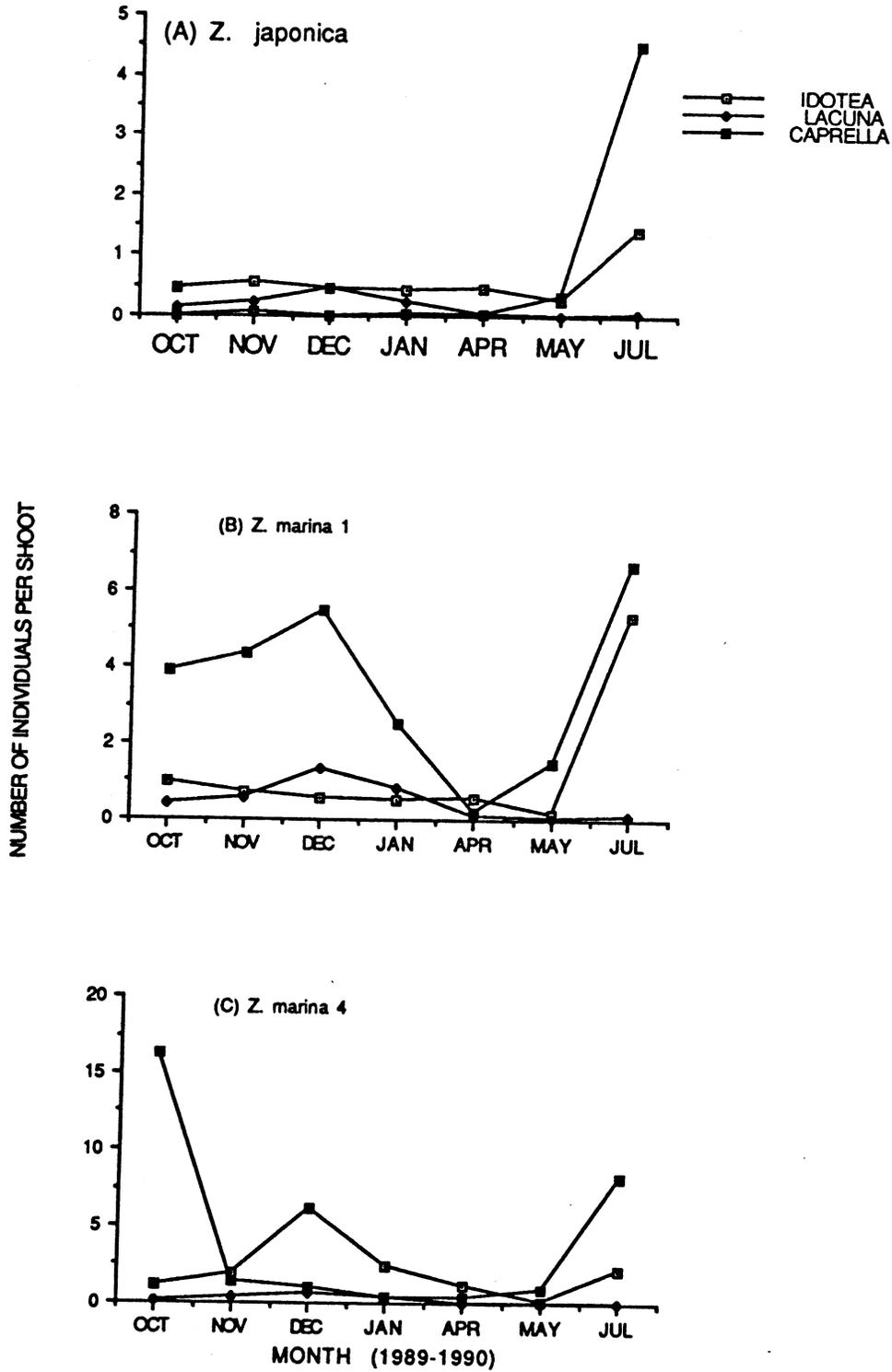


Figure 7. Temporal variation in average number of individuals of grazers per eelgrass shoot at each of the three sites.

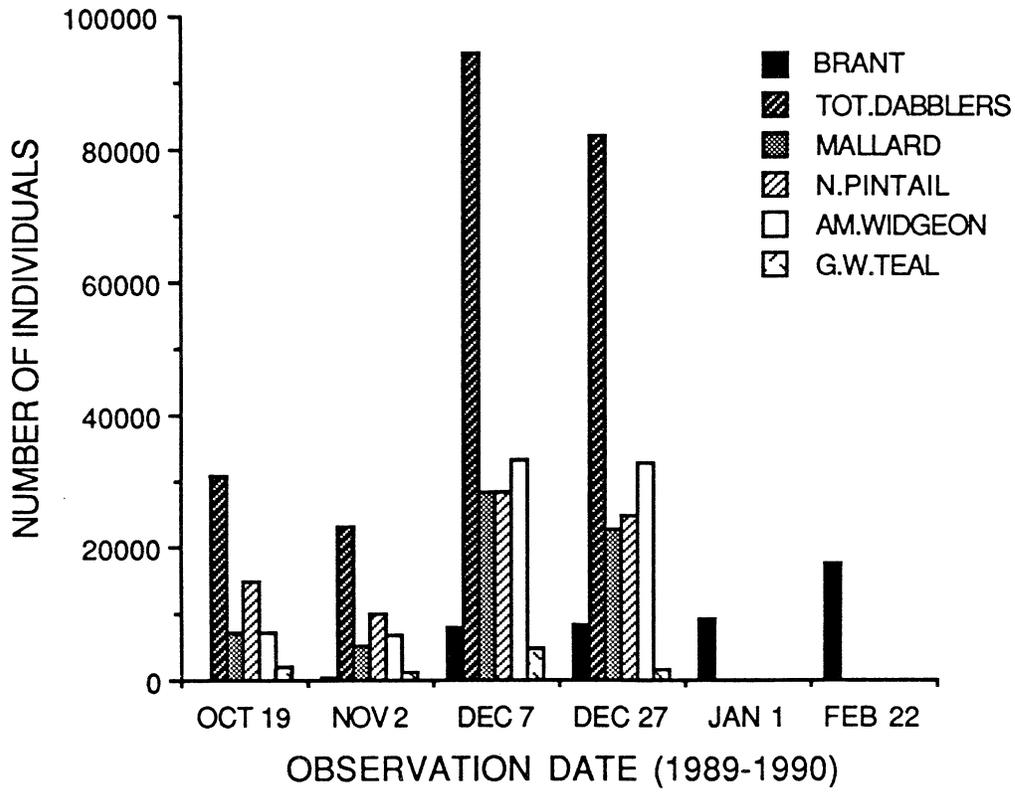


Figure 8. Temporal variations in grazing bird abundances in Padilla Bay.

Table 1. Annual grazing estimates for *Idotea* and birds in the seagrass system. Total average system annual NPP is 351 gC m⁻² (Thom 1990a). Total area covered by *Z. japonica* = 481 ha; total area covered by *Z. marina* = 2,526 ha. Total annual productivity for the *Z. japonica* subsystem = 317 x 10³ kgC. Total annual productivity for the *Z. marina* subsystem = 10,240 x 10³ kgC. Total system annual productivity = 10,557 x 10³ kgC.

	NPP		
	gC m ⁻²	Total (x10 ³ kgC)	% of total
<i>Idotea</i>			
<i>Z. japonica</i>	246.4	1,185	374 ^a
<i>Z. marina</i>	38.2	964	9.4 ^b
Total <i>Idotea</i>	--	2,149	20.4
Mallard	1.322	40	0.4
Northern pintail	1.310	40	0.4
American widgeon	1.218	37	0.4
Green winged teal	0.083	2	<0.1
Black brant	1.320	40	0.4
Total birds	5.253	159	1.5
Total grazed	—	2,308	21.9

^a*Z. japonica* subsystem only.

^b*Z. marina* subsystem only.

