# EVISCERATION BEHAVIOUR AND THE SEASONAL INCIDENCE OF EVISCERATION IN THE HOLOTHURIAN EUPENTACTA QUINQUESEMITA (SELENKA)

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#### ABSTRACT

Evisceration of the dendrochirote holothurian Eupentacta quinquesemita (Selenka) results from softening of three autotomy structures, the P-L tendon, the intestine-cloacal junction and the introvert. The internal organs are expelled anteriorly through rupture of the introvert. Visceral autotomy occurs under natural conditions and is seasonal. Evisceration started in September and continued through November. By November 1982, 76% of the holothurians at one site and 49% at a second site had eviscerated. Specimens collected in the following winter months had regenerating or newly functional digestive tracts. Regeneration under natural conditions takes approximately 2-4 weeks. The extent of annual evisceration appears to be variable from year to year. Seasonal evisceration may serve as an economic autotomy excretory mechanism, whereby waste-laden digestive tracts are discarded after an active summer of feeding. The induction of autumnal evisceration is probably a complex interaction of internal and environmental factors. During the spring and summer the incidence of evisceration decreased or was absent and its occurrence during these months may be in response to asteroid predation.

## INTRODUCTION

Evisceration is a form of autotomy practiced by many holothurian echinoderms and involves ejection of the digestive tract and other internal organs (Emson & Wilkie 1980). Dendrochirote holothurians eviscerate anteriorly by rupture of the introvert with loss of the tentacular crown, digestive tract, haemal vessels and sometimes gonads as well (Pearse 1909, Kille 1935, Tracey 1972, Smith & Greenberg 1973). Aspidochirote holothurians eviscerate posteriorly, ejecting the digestive tract, haemal vessels, and sometimes gonads and respiratory trees through a cloacal rupture (Domantay 1931, Dawbin 1949, Mosher 1956, Bai 1971, Jespersen & Lützen 1971). Evisceration has been investigated in the laboratory in numerous studies (Pearse 1909, Bertolini 1930, 1932, Domantay 1931, Kille 1935,

1936, Dawbin 1949, Bai 1971, Jespersen & Lützen 1971, Smith & Greenberg 1973), but we have no information on the stimuli inducing evisceration in the field. The picture is further obscured by the incidence of seasonal visceral absence reported to be widespread in some aspidochirote holothurian populations (Bertolini 1930, Swan 1961, Mosher 1965, Jespersen & Lützen 1971, Dimock 1977, Muscat 1982, Yingst 1982). Examination of the gut condition of two aspidochirote species revealed that seasonal visceral atrophy occurs (Tanaka 1958, Fankboner *et al.* 1981). Evisceration has been suggested to serve as a predator diversion device, an excretory mechanism and a means of reducing metabolic costs in adverse conditions (Domantay 1931, Mosher 1956, Tracey 1972). The functional and physiological significance of visceral autotomy and atrophy are particularly curious in cases where it is seasonal.

Eupentacta quinquesemita (Selenka) is a small (50-100 mm), common dendrochirote holothurian found subtidally along the northwest coast of North America. This species is known to eviscerate if handled roughly (Kozloff 1973). In this investigation, the evisceration behaviour of E. quinquesemita is described and compared with that documented for two other dendrochirote holothurians (Kille 1935, Tracey 1972). Preliminary examination of this species revealed that visceral autotomy occurs in the field. Therefore, monthly collections were made at two sites to investigate the incidence and seasonality of evisceration, and to examine factors leading to induction of evisceration under natural conditions. Because gonads are expelled during evisceration in some holothurians (Bertolini 1932, Dawbin 1949, Jespersen & Lützen 1971, Tracey 1972, Chaffe 1982), specimens of E. quinquesemita were examined for the presence of gonads to investigate the influence of evisceration on reproduction.

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## STUDY SITES

The two study sites were Ten Mile Point (TMP) and the Royal Victoria Yacht Club (RVYC), both near Victoria, B.C. Canada (Fig. 1). TMP has a bedrock substrate and is subject to strong tidal currents with flow ranging from low speeds at slack tide to  $180\text{-}200 \, \text{cm/sec}$  during maximal flow (Thomson 1981). At TMP specimens of Eupentacta quinquesemita were found within crevices or on the substrate surface at a density of  $780/\text{m}^2$  (SD = 300). The RVYC is in a protected bay where current conditions are usually mild and the holothurians were found attached to the undersides of the marina floats at a density of  $140/\text{m}^2$  (SD = 132).

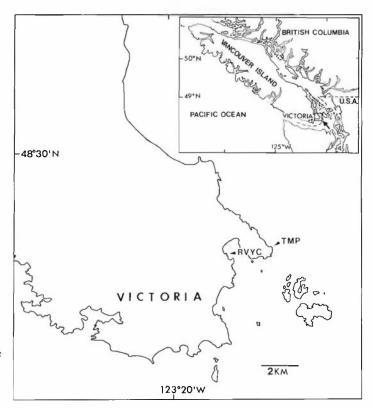


Fig. 1. Location of the Ten Mile Point and Royal Victoria Yacht Club study areas.

## MATERIALS AND METHODS

Specimens of *E. quinquesemita* were collected using SCUBA and placed in plastic bags filled with ambient sea water to prevent evisceration during transport. The bags were securely sealed for transport to the laboratory. Monthly collections were made from November 1981 through March 1983. It appeared that evisceration in the field occurred prior to November 1981, consequently bimonthly collections were made during September and October 1982. Due to the great difference in population density of the two sites, the monthly sample size collected from TMP was larger; 50-100 animals were collected from TMP and 20-60 from the RVYC.

The viscera of collected specimens were examined by dissection and categorized as absent (A), regenerating (R), newly functional (NF), or well developed (WD). The criteria for NF viscera were, gut regions (Fig. 2) easily distinguished, and the presence of detrital material in the gut was considered to be an indication of resumed feeding. Newly functional digestive tracts are white or pale yellow and this was used to distinguish them from older digestive tracts which are typically brown. Contingency table analysis was used to test for significant differences in the

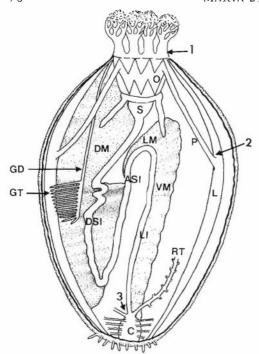


Fig. 2. Diagrammatic internal anatomy of Eupentacta quinquesemita (Selenka) autotomy regions: (1) introvert; (2) P-L tendon; (3) intestine-cloacal junction.

ASI, ascending small intestine; C, cloaca; DM, dorsal mesentery; DSI, descending small intestine; GD, gonoduct; GT, gonad tubules; L, longitudinal body wall muscle; LI, large intestine; LM, lateral mesentery; O, ossicles; P, pharyngeal retractor muscle; S, stomach; RT, respiratory tree; VM, ventral mesentery.

monthly proportions of functional (NF+WD) and non-functional (A+R) specimens between the two sites. The presence of gonads was monitored monthly by a subjective method. Two categories were established, 0-50% and 50-100% of the perivisceral coelomic space occupied by gonad. This rough index proved sufficient to detect whether gonads were expelled during evisceration. Examination of dissected holothurians revealed that the endoparasitic gastropod  $Thyonicola\ americana$  was attached to the intestine of some specimens, and the presence or absence of these parasites was recorded.

To study evisceration behaviour, the response was elicited in the laboratory by injection of 0.5 ml of 0.45 M KCl (isosmotic with local sea water) into the perivisceral coelom with a tuberculin syringe. The sequence of evisceration events was recorded photographically. Spontaneous evisceration behaviour was also observed in the field.

Asteroid predation of *E. quinquesemita in situ* was investigated at TMP. All sea stars encountered during three dives were turned over, and their oral surface was examined. If the cardiac stomach was extruded, it was examined for the presence of *E. quinquesemita*, and the tube feet were examined for holothurians being transported toward the mouth. No attempt was made to determine stomach contents of sea stars with retracted cardiac stomachs. Large sea-water tables, supplied with running ambient sea water, at the Friday Harbor Laboratories (University of Washington) were used to study the predator-prey interactions of the asteroid *Solaster stimpsoni* and *E. quinquesemita* 

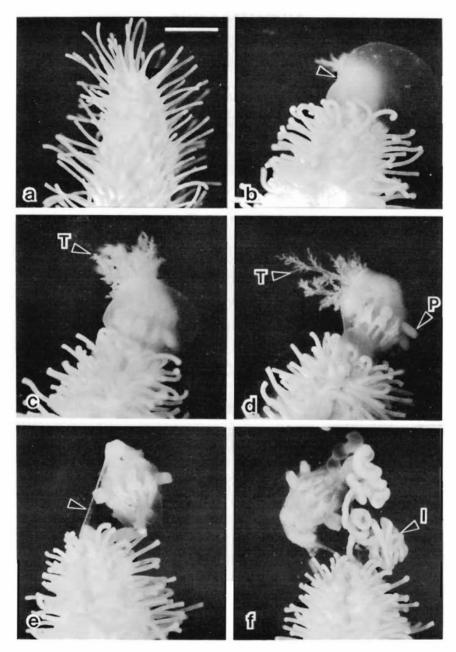


Fig. 3. Evisceration response series. (a) anterior end of specimen before KCl injection, scale = 1.0 cm. (b-f) evisceration response to 0.45 M KCl injection. (b) 1.5 min. Softening and distension of the introvert (arrowhead). (c) 3.0 min. The oral complex is visible through the softened introvert. T, tentacles. (d) 4 min. The introvert has ruptured. P, autotomized PRM; T, tentacles. (e) 8 min. A single strand of introvert tissue is connected to the body wall (arrowhead). (f) 10 min., visceral expulsion. I, intestine.

## RESULTS

## Evisceration behaviour

Evisceration always resulted from autotomy of three tissues: 1) the introvert (anterior extensible portion of body wall); 2) the tendons connecting the pharvngeal retractor muscles (PRMs) to the longitudinal body wall muscles (LBWMs) (P-L tendons) and 3) the intestine-cloacal junction (Fig. 2). Isosmotic KCl induced evisceration (N = 10), and the initial reaction (within 30 sec) was a general longitudinal body contraction, especially apparent anteriorly due to PRM contraction (Figs 3a, b). This was followed by autotomy of the P-L tendons and the intestinecloacal junction. The autotomized viscera and PRMs were visible once introvert distension started (Figs 3b, c). The autotomy sequence of the P-L tendons was variable. In some specimens, the tendons autotomized simultaneously, and in others two or three autotomized before the rest. The digestive tract detached from its supporting mesentery creating a free mesenteric edge. During evisceration the introvert changed from a firm opaque structure to a soft translucent one, through which the calcareous ring and autotomized viscera were visible (Fig. 3c). The introvert swelled as it received viscera and coelomic fluid propelled forward by contraction of the body wall muscles. Introvert distension usually started within 30 sec of injection, but took up to 5 min in some specimens ( $\bar{X}_{10} = 2.4$  min, SD = 1.7 min). Rupture of the introvert resulted in expulsion of coelomic fluid and eventually the introvert detached along its posterior edge where it joins with the body (Figs 3d-f). Detachment of the introvert, freeing the viscera from their last

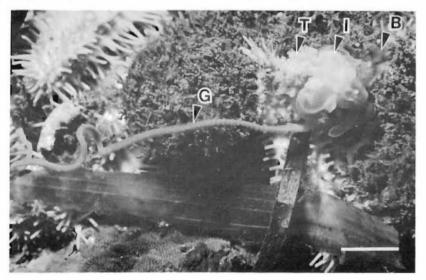


Fig. 4. Evisceration of E. quinquesemita in the field. The gut (G) is being dragged to the left by current. B, body of specimen; I, introvert; T, tentacles, scale = 1.0 cm.

attachment to the body, took up to 12 hr in some aquarium specimens, although once the introvert softened it was easily removable. Detachment of the viscera in situ is probably effected by an external agent such as current flow or turbulence (Fig. 4). Evisceration resulted in loss of the tentacles, aquapharyngeal bulb, digestive tract and associated haemal vessels. Variable amounts of gonad were expelled, and the amount depended on gonad development. Specimens with well-developed gonads eviscerated numerous tubules, especially those entangled with the viscera. The only other organs retained following evisceration were the respiratory trees.

Spontaneous evisceration in the field (see below) follows the same behavioural sequence as observed in the laboratory. It was not possible to time the sequence of internal autotomy, but introvert autotomy appeared to take longer in the field compared with laboratory observations. Specimens with autotomizing introverts were observed for 10-20 min, but rupture and detachment of the introvert were not observed. On the same occasion, specimens with nearly detached viscera (Fig. 4) and completely detached viscera and tentacles were observed.

## Incidence of evisceration in the field

Frequency histograms (Fig. 5) of the proportions of *E. quinquesemita* with absent, regenerating and newly functional viscera show that evisceration was seasonal at both study areas. A high incidence of specimens lacking digestive tracts occurred

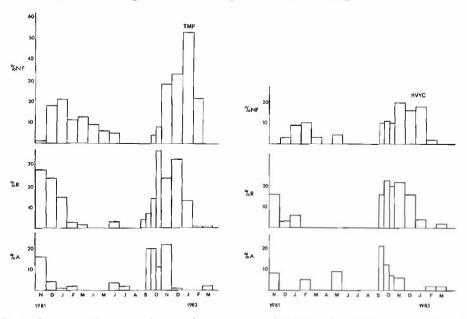


Fig. 5. Frequency histograms showing the percentages of RVYC and TMP E. quinquesemita with absent (A), regenerating (R), and newly functional viscera (NF); November 1981-March 1983. The remaining percentages to make a total of 100% comprise of specimens with normal viscera.

during autumn 1981 and 1982. The 1982 data are more complete and so are described in detail. Samples taken throughout the autumn contained specimens that lacked viscera and others with well-developed digestive tracts. The TMP population exhibited a high incidence of evisceration from September 10 through November 14. Evisceration of the RVYC population appeared to be a more sharply defined event with the highest proportion of specimens lacking viscera between September 6-20, coincident with the onset of evisceration at TMP. The proportion of holothurians with regenerating viscera at TMP increased following evisceration and remained high as the number of eviscerated specimens decreased. The RVYC population exhibited a relatively uniform level of regenerating specimens through December. A high proportion of holothurians with newly functional viscera was present November through January at the RVYC and November through February at TMP. During spring and summer, the incidence of evisceration decreased to a low level or was absent.

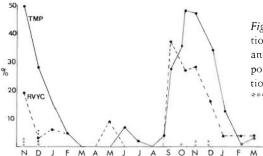


Fig. 6. Proportions of specimens lacking functional viscera (A + R) in the TMP (solid line) and the RVYC (broken line) samples. The proportions differ significantly in the two populations where marked: \* (P < 0.05), \*\* (P < 0.02), \*\*\* (P < 0.01).

The sequential timing of evisceration and regeneration was similar in the two populations except for significant differences during November-December 1981 and October-December 1982 when the incidence of evisceration was greater at TMP (Fig. 6). Although the 1981 data are not complete, it appears that the incidence of evisceration in autumn 1981 was lower at both study sites (Fig. 5). The maximal monthly proportions of specimens with non-functional viscera (A+R) in 1982 were 38% in September for the RVYC and 48% in October for TMP (Fig. 6). By November 1982, 76% of the TMP population had eviscerated and 49% of the RVYC had eviscerated. Thus, substantial proportions of these populations were unable to feed during this time. By January, the proportions of non-feeding holothurians decreased to 13% at TMP and 4% at RVYC (Fig. 6). The histogram data (Fig. 5) can be used to estimate a regeneration timetable for E. quinquesemita following seasonal evisceration. Holothurians with newly functional digestive tracts were first observed in October, 2 weeks after the onset of evisceration and high proportions of newly functional specimens were present from November onwards. This suggests that regeneration following visceral autotomy takes approximately 2-4 weeks.

## Field observations

The first observation of visceral autotomy in the field during the 1982 evisceration season was made on September 10 at TMP (Fig. 4), although no evidence of evisceration was found in the sample collected at the same time. Holothurians in the process of evisceration (N=7) and detached viscera and tentacles on the substrate surface (N=20) were particularly abundant at TMP on September 24. The sample collected on this occasion contained a high proportion of specimens lacking viscera. Most of the autotomized viscera were partially decomposed. This suggests that immediate visceral consumption by predators or scavengers was not occurring, although potential predators including Solaster stimpsoni and Dermasterias imbricata (see below) were present. Evisceration in the field was not observed at the RVYC.

# Evisceration of gonads

Frequency histograms show the proportions of *E. quinquesemita* with gonads occupying at least 50% of the coelomic space (Fig. 7). The decrease in gonad content of specimens from February through April for TMP and the sharp drop in April for the RVYC correspond with the spring spawning of *E. quinquesemita* (Byrne 1983). During the summer, the gonad size increased, and through the autumn most specimens had gonads occupying at least 50% of the coelomic space (Fig. 7). The coelom of eviscerated holothurians was usually filled with gonad.

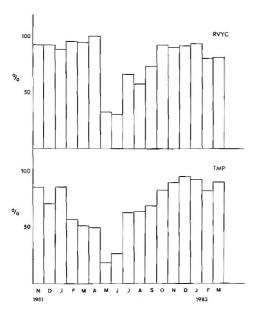


Fig. 7. Histograms showing the percentages of E. quinquesemita at TMP and the RVYC with gonads occupying 50-100 % of the coelomic space during November 1981-March 1983. This rough index demonstrates spring spawning followed by summer increase in gonad size that is maintained through autumn and winter, despite evisceration.

Therefore, although some tubules may be expelled during evisceration in the field, most of the gonad is retained. Although the gonads were not examined microscopically, it did not appear that gonad resorption occurred during regeneration.

## Endoparasitism

At TMP, 41% (N = 924) of the holothurians with well-developed viscera had *Thyonicola americana* attached to the intestine, whereas only 0.9% (N = 442) of the RVYC specimens had the parasite. *T. americana* is a member of the Family Entoconchidae, shell-less vermiform prosobranchs, many of which are holothurian endoparasites (Lützen 1979). The parasites grow within the coelom and at maturity are 2-3 times the length of the host (Byrne 1985b). They rarely filled the coelom, but occasionally *E. quinquesemita* contained numerous mature parasites which completely obliterated the coelomic space. Although not quantified, it appeared that *E. quinquesemita* infected by numerous mature parasites were more prone to eviscerate during collection and handling than less infected hosts. Recently autotomized viscera found in collection bags and in aquaria soon after introduction of holothurians were often from specimens with a high parasite load.

# Predation on E. quinquesemita

The oral surfaces of three commonly encountered asteroid species, Solaster stimpsoni, Dermasterias imbricata and Pycnopodia helianthoides were examined in the field. All three species prey on E. quinquesemita (Table 1). The holothurians were observed being transported by the asteroid's tube feet towards the mouth or engulfed in extruded stomach folds. D. imbricata preyed on small (<20 mm long) E. quinquesemita. A single specimen of P. helianthoides was observed extruding its stomach over a clump of E. quinquesemita, and the holothurians as a group were being digested. It was not possible to determine whether evisceration had occurred during the predator-prey encounters because the specimens were engulfed in stomach folds and most were partially digested. In July 1983, a single S. stimpsoni was observed with E. quinquesemita viscera held by its tube feet, and the eviscerated holothurian had retracted into a crevice underneath the asteroid.

To study predator-prey interactions in the laboratory, eight *E. quinquesemita* were placed inside empty tests of the large barnacle *Balanus nubilis* and allowed to acclimate in a sea-water tray before introduction of two *S. stimpsoni*. One of the asteroids found the holothurians within 5 hr and adopted a feeding posture, arching over them and extruding its cardiac stomach. Two of the holothurians eviscerated while being attacked. Examination of the oral surface of the asteroid revealed the autotomized viscera being transported towards the mouth by the tube feet and within the stomach folds (Fig. 8). The holothurians retracted into the barnacle where they were unavailable to the sea star and eventually the six holothurians

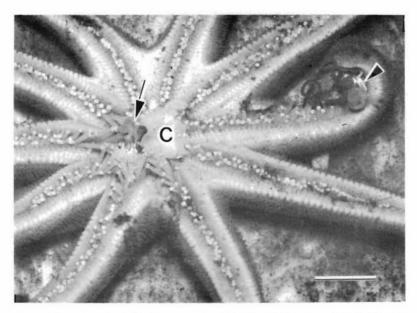


Fig. 8. The oral surface of Solaster stimpsoni Verrill with the viscera expelled by two E. quinquesemita in the laboratory. One of the expelled viscera (arrow) is engulfed in the asteroid's cardiac stomach (C), and the second is held within an arm loop (arrowhead) being transported orally by the tube feet. The holothurians retracted into the barnacle test (see text) and were not available to the asteroid. Scale = 4 cm.

that did not eviscerate, protracted their tentacles to feed. The second *S. stimpsoni* did not approach the holothurians. In another experiment, twelve *E. quinquesemita* attached to tubes of the polychaete *Eudistylia vancouveri* were placed in a sea-water tray, and two *S. stimpsoni* were introduced. Within 12 hr each asteroid was consuming an entire *E. quinquesemita*. In this experiment the holothurians did not have a refuge into which they could retract.

Touching the tube feet and arms of *S. stimpsoni* to the tentacles and body of *E. quinquesemita* (8 in the field and 5 in aquaria) elicited tentacle retraction, but not evisceration. Evisceration was elicited only if the asteroid adopted an arched feeding posture over the holothurians and extruded its cardiac stomach.

#### DISCUSSION

The evisceration behaviour of Eupentacta quinquesemita is similar to that described for two other dendrochirote holothurians, Sclerodactyla briareus and Thyone okeni (Pearse 1909, Kille 1935, Tracey 1972, Smith & Greenberg 1973) and involves anterior autotomy of the tentacular crown and viscera, through the breakdown of three connective tissue autotomy structures (Byrne 1982, 1985a). The invariability of the autotomy sites associated with evisceration and the ease

with which the body parts are discarded are characteristic of echinoderm autotomy (Emson & Wilkie 1980). Gonad expulsion was not observed for S. briareus (Kille 1935) but was observed for T. okeni (Tracey 1972). The amount of gonadal material eviscerated by E. quinquesemita in vitro varied, depending on gonad development. Field collections revealed that most of the gonad tubules are retained during seasonal evisceration, which is obviously important to spring spawning. Gonad resorption does not appear to occur during visceral regeneration.

Observation of spontaneous evisceration from numerous holothurians in situ has not been reported previously and this is the first observation of seasonal evisceration for a dendrochirote holothurian. Evisceration of *E. quinquesemita* appears to be a cyclic phenomenon occurring annually in the autumn. There are numerous reports of autumnal evisceration for aspidochirote holothurians (Bertolini 1930, Swan 1961, Mosher 1965, Jespersen & Lützen 1971, Dimock 1977, Muscat 1982, Yingst 1982).

Regeneration in the field following seasonal evisceration appears to take approximately 2-4 weeks, similar to the regeneration time of *S. briareus* following artificially induced evisceration (Kille 1935), but shorter than the 6 weeks reported for *T. okeni* (Tracey 1972). An aspidochirote holothurian that occurs at TMP, *Stichopus californicus*, also exhibits seasonal visceral absence, and regeneration in this species also takes 2-4 weeks under the same ambient conditions as those for *E. quinquesemita* (Fankboner & Cameron in prep.).

Annual evisceration imposes a seasonality on feeding, but feeding in winter may not be important to *E. quinquesemita*, since during these months there is a decrease in suspended food material (Hobson 1981). A seasonal change in feeding behaviour was observed for *Stichopus tremulus*, which fasts just prior to annual visceral absence (Jespersen & Lützen 1971). *Leptopentacta elongata* ceases to feed during the winter, although this species retains its digestive tract (Fish 1967). *Aslia lefevrei* and *Neopentadactyla mixta* also decrease their feeding activity during the winter and this is associated with torpor in *N. mixta* (Costelloe & Keegan 1984, Smith & Keegan, in press). Visceral atrophy occurs in *Stichopus japonicus* and *S. californicus* in late summer and autumn (Tanaka 1958, Fankboner *et al.* 1981). It seems reasonable that the least disadvantageous time to lack a digestive tract is in the autumn when stored reserves are probably high after a summer of feeding activity, and at the onset of decreased food abundance.

Annual evisceration of *E. quinquesemita* occurs irrespective of parasitic infection. The parasites are expelled along with the host's viscera and this interferes with their life cycle (Byrne 1985b). *S. tremulus* is also host to entoconchid parasites, and exhibits autumnal evisceration irrespective of parasite infection (Lützen 1979). Abundant *T. americana* in the coelom appear to make *E. quinquesemita* more prone to eviscerate, although the parasite is itself not a trigger. The parasite infected a substantial portion of TMP specimens and was virtually absent from the RVYC. Parasitic infection may, at least in part, be a factor influencing the higher

incidence of evisceration at TMP. The incidence of evisceration at TMP in autumn 1982 surpassed that at the RVYC by 25%.

Evisceration in summer may be due to factors different from those involved with the seasonal cycle, perhaps associated with predation. Evisceration in *E. quinquesemita* appears to serve in asteroid predator diversion, but its success depends on the presence of a refuge into which the rest of the holothurian can retract while the starfish consumes the freed visceral mass. The presence of whole individuals being consumed in the field shows that evisceration is not always successful in avoiding predation, presumably due to a lack of refuge. *Solaster stimpsoni* appears to restrict its diet to holothurians, including *E. quinquesemita* (Mauzey *et al.* 1968) and so evisceration may be an important evasive response to this asteroid *in situ*. Engstrom (1974) also observed evisceration of *E. quinquesemita* in response to this asteroid. The stimuli eliciting the response in asteroid predator-holothurian prey encounters may be mechanical (tube feet activity) and/or chemical (digestive enzymes or other stomach secretions).

It has been suggested that evisceration may be too slow to be of use in predator diversion (Dawbin 1949). Evisceration by *E. quinquesemita* in the field appears to take twenty minutes or more and may not be useful in diverting fast predators such as fish, but does appear to divert asteroids. Gonad tubules of *E. quinquesemita* ingested by fish in aquaria were rapidly rejected (personal observation). This suggests that *E. quinquesemita* may be unpalatable to fish, as found for other holothurians (De Vore & Brodie 1982). The expelled viscera were not being consumed in the field and, as observed for *Stichopus tremulus*, may be unpalatable to numerous benthic predators or scavengers (Lützen 1979).

The functional significance of annual autotomy of the digestive tract and feeding apparatus is not clear. *E. quinquesemita*, like other holothurians does not have an excretory system as such (Hyman 1955, Jangoux 1982). Much of the particulate waste material is taken up by amoebocytes and accreted into brown bodies, some of which are deposited in the gut wall (Byrne 1983), as reported for other holothurians (Hetzel 1965). The brown colour of older intestines appears to be associated with brown body deposition. Lipofuscins are associated with brown bodies (Fontaine & Lambert 1973) and in vertebrate tissues are called wear-and-tear pigments, often associated with disease (Pearse 1972). Evisceration under these circumstances may be a form of economic autotomy; perhaps retaining viscera laden with waste accumulations is a greater metabolic load than that of regeneration itself. That evisceration serves as a means of excretion has been suggested (Tracey 1972).

The digestive tract condition prior to annual visceral absence has been examined for two aspidochirote species, *Stichopus japonicus* and *S. californicus* (Tanaka 1958, Fankboner *et al.* 1981). The studies revealed that digestive tract atrophy takes place and it appears that seasonal evisceration does not occur in *S. californicus* (Fankboner *et al.* 1981). However, it is possible that for some holothurians

visceral atrophy may be a prelude to evisceration. That seasonal evisceration does not occur in *S. californicus* suggests that aspidochirote and dendrochirote holothurians that lack digestive tracts in the autumn, deal with digestive tract maintenance by different methods, with visceral atrophy in aspidochirotes and visceral autotomy in dendrochirotes. This speculation has to be substantiated by similar investigations of other holothurians.

Evisceration in *E. quinquesemita* was coincident at the two study areas, but did not occur in 100% of the populations. The extent of annual evisceration differed in the TMP and RVYC populations and also appeared to differ in 1981 and 1982. Therefore, individual holothurians may not eviscerate every year. For some aspidochirote populations, virtually 100% of the holothurians were reported to lack digestive tracts in the autumn. This is true for *S. regalis* (Bertolini 1932) and *S. californicus* (Swan 1961, Fankboner & Cameron in prep.). The stimulus that elicits seasonal evisceration in some *E. quinquesemita* and not others is unknown. Occurrence of evisceration in the autumn might be determined by a complex of factors such as age, feeding activity and recent (i.e., summer) evisceration. These factors would influence brown body accumulation and possibly gut degeneration.

Some holothurian species do not appear to eviscerate and other species that can be induced to eviscerate *in vitro*, do so rarely under natural conditions (Bertolini 1932, Kille 1936, Dawbin 1949, Mosher 1965). Why some species eviscerate and others do not is not known. Seasonal evisceration and gut auto-degeneration may be associated with an internal rhythm and perhaps cued by environmental factors. The timing of evisceration in *E. quinquesemita*, as for other holothurians that exhibit annual visceral absence, coincides with the autumn solstice. Perhaps decreasing day length is a contributing stimulus. The decrease in food abundance during the autumn may also be an important environmental stimulus. Internal factors influencing seasonal evisceration might include accumulation of waste (toxic?) products, gut degeneration and the build up of body wall and gonadal reserves. Induction of seasonal evisceration is likely due to a complex interaction of internal and external factors.

## REFERENCES

- Bai, M.M., 1971. Regeneration in the holothurian, Holothuria scabra Jager. Indian J. exp. Biol. 9: 467-471.
- Bertolini, F., 1930. Rigenerazione dell'apparato digerente nello Stichopus regalis. Pubbl. Staz. zool. Napoli 10: 439-447.
- Bertolini, F., 1932. Rigenerazione dell'apparato digerente nelle Holothuria. Pubbl. Staz. zool. Napoli 12: 432-447.
- Byrne, M., 1982. Functional morphology of a holothurian autotomy plane and its role in evisceration.

   In J.M. Lawrence (ed.): International Echinoderms Conference, Tampa Bay, pp. 65-68. A.A. Balkema, Rotterdam.

Byrne, M., 1983. Evisceration amd autotomy in the holothurian Eupentacta quinquesemita (Selenka). – Ph. D. Thesis, University of Victoria.

Byrne, M., 1985a. The mechanical properties of the autotomy tissues of the holothurian Eupentacta quinquesemita (Selenka) and the effects of certain physico-chemical agents. – J. exp. Biol. 117 (in press).

Byrne, M., 1985b. The life history of the gastropod *Thyonicola americana* Tikasingh, endoparasitic in a seasonally eviscerating host. – Ophelia 24: 91-101.

Chaffe, C., 1982. Birth by the viviparous holothuroid *Pachythyone rubra* (Clark, 1901). – In J.M. Lawrence (ed.): International Echinoderms Conference, Tampa Bay, pp. 465-466. A.A. Balkema, Rotterdam.

Costelloe, J. & B.F. Keegan, 1984. Feeding and related morphological structures in the dendrochirote Aslia lefevrei (Holothuroidea: Echinodermata). – Mar. Biol. 84: 135-142.

Dawbin, W.H., 1949. Auto-evisceration and the regeneration of viscera in the holothurian Stichopus mollis (Hutton). - Trans. R. Soc. N.Z. 77: 497-523.

De Vore, D.E. & E.D. Brodie, Jr., 1982. Palatability of the tissues of the holothurian Thyone briareus Lesueur) to fish. – J. exp. mar. Biol. Ecol. 61: 279-285.

Dimock, R.V., 1977. Effects of evisceration on oxygen consumption by Stichopus parvimensis (Echinodermata: Holothuroidea). – J. exp. mar. Biol. Ecol. 28: 125-132.

Domantay, J.S., 1931, Autotomy in holothurians. – Nat. appl. Sci. Bull. Univ. Philipp. 1: 389-404. Emson, R.H. & I.C. Wilkie, 1980. Fission and autotomy in echinoderms. – Oceanogr. mar. Biol. Ann. Rev. 18: 155-250.

Engstrom, N.A., 1974. Population dynamics and prey-predation relations of a dendrochirote holothurian, Cucumaria lubrica, and sea stars in the genus Solaster. - Ph. D. Thesis, University of Washington.

Fankboner, P.V., G.L. Cameron & T. Smith, 1981. Annual loss of the gut by the sea cucumber Parastichopus californicus (Stimpson). - (Abstract). - W.S.N. Annual Meeting, Santa Barbara, p. 18. Fish, J.D., 1967. The biology of Cucumaria elongata (Echinodermata: Holothuroidea). - J. mar.

biol. Ass. U.K. 47: 129-143.

Fontaine, A.R. & P. Lambert, 1973. The fine structure of the haemocyte of the holothurian, Cucumaria miniata (Brandt). - Can. J. Zool. 51: 323-332.

Hetzel, H.R., 1965. Studies on holothurian coelomocytes. II. The origin of coelomocytes and the formation of brown bodies. – Biol. Bull., Woods Hole 128: 102-111.

Hobson, L.A., 1981. Seasonal variations in maximum photosynthetic rates of phytoplankton in Saanich Inlet, Vancouver Island, British Columbia. — J. exp. mar. Biol. Ecol. 52: 1-13.

Hyman, L.H., 1955. The Invertebrates: Echinodermata, pp. 228-230. McGraw-Hill, New York. Jangoux, M., 1982. Excretion. – In M. Jangoux & J.M. Lawrence (eds): Echinoderm Nutrition, pp. 437-448. A.A. Balkema, Rotterdam.

Jespersen, A. & J. Lützen, 1971. On the ecology of the aspidochirote sea cucumber Stichopus tremulus (Gunnerus). – Norw. J. Zool. 19: 117-132.

Kille, F.R., 1935. Regeneration in Thyone briareus Lesueur following induced autotomy. – Biol. Bull., Woods Hole 69: 82-108.

Kille, F.R., 1936. Regeneration in holothurians. - Carnegie Inst. Wash. Yrb. 35: 85-86.

Kozloff, E.N., 1973. Seashore life of Puget Sound, the Strait of Georgia and the San Juan Archipelago, p. 99. J. J. Douglas Ltd, Vancouver.

Lützen, J., 1979. Studies on the life history of Enteroxenos Bonnevie, a gastropod endoparasitic in aspidochirote holothurians. — Ophelia 18: 1-51.

Mauzey, K.P., C. Birkeland & P.K. Dayton, 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. – Ecology 49: 603-619.

Mosher, C., 1956. Observations on evisceration and visceral regeneration in the sea-cucumber, Actinopyga agassizi Selenka. – Zoologica, N.Y. 41: 17-26.

- Mosher, C., 1965. Notes on natural evisceration of the sea cucumber Actinopyga agassizi Selenka. Bull. mar. Sci. 15: 255-258.
- Muscat, A.M., 1982. The population biology and ecology of Parastichopus parvimensis, a deposit feeding holothurian. In J.M. Lawrence (ed.): International Echinoderms Conference, Tampa Bay, p. 319. A.A. Balkema, Rotterdam.
- Pearse, A.G.E., 1972. Histochemistry theoretical and applied. Vol. 2, pp.1076-1093. Churchill Livingstone, London. 1512 pp.
- Pearse, A.S., 1909. Autotomy in holothurians. Biol. Bull., Woods Hole 18: 42-49.
- Smith, G.N., Jr. & M.J. Greenberg, 1973. Chemical control of the evisceration process in Thyone briareus. Biol. Bull., Woods Hole 144: 421-436.
- Smith, T. & B.F. Keegan, (in press). Seasonal torpor in Neopentadactyla mixta (Östergren), (Echinodermata, Holothuroidea). In B.F. Keegan (ed.): International Echinoderms Conference, Galway.
- Swan, E.F., 1961. Seasonal evisceration in the sea cucumber, Parastichopus californicus (Stimpson). Science, N.Y. 133: 1078-1079.
- Tanaka, Y., 1958. Feeding and digestive processes of Stichopus japonicus. Bull. Fac. Fish. Hokkaido Univ. 9: 14-26.
- Thomson, R.E., 1981. Oceanography of the British Columbia coast. Can. Spec. Publ. Fish. aquat. Sci. 56: 188-195.
- Tracey, D.J., 1972. Evisceration and regeneration in Thyone okeni (Bell, 1884). Proc. Linn. Soc. N.S.W. 97: 72-81.
- Yingst, J.Y., 1982. Factors influencing rates of sediment ingestion by Parastichopus parvimensis (Clark), an epibenthic deposit-feeding holothurian. Estuar. coast. Shelf Sci. 14: 119-134.