

# Natural and disturbance-induced demographic variation in an infaunal polychaete, *Nephtys incisa*

Roman N. Zajac<sup>1</sup>, Robert B. Whitlatch<sup>2</sup>

<sup>1</sup> Graduate Program in Environmental Sciences, The University of New Haven, 300 Orange Avenue, West Haven, Connecticut 06516, USA

<sup>2</sup> Department Marine Sciences, The University of Connecticut, Avery Point, Groton, Connecticut 06340, USA

**ABSTRACT:** Demography of the infaunal polychaete *Nephtys incisa* was investigated for periods of 1 yr prior to and following disturbance (dredge material disposal) at a site in central Long Island Sound, USA. Infaunal grab samples were taken at 5 stations 200 m to 3 km apart. The demography of populations at each station was based on age-classes spanning juveniles to adults 4+ yr of age. Age-specific survivorship and fecundity were based on changes in mean density of each cohort and a positive correlation between female size and egg production, respectively. Analyses of population matrix models indicated pre-disposal populations had positive population growth rates, despite differences in vital rates among stations. During the second year, population growth rates were reduced by 50%, below population maintenance levels, at each station, primarily due to recruitment failure across the entire study site. Population growth rates were reduced an additional 25% by disturbance at the dump site and next closest station (200 m away) due to decreased worm size and survivorship relative to other stations, and the absence of recolonization by worms > 2 yr of age. Populations of *N. incisa* appear to experience several demographic 'states', related to periods of potential population growth, decline and recovery from disturbance. Based on analyses of related demographic parameters, there is a concomitant change in the contribution different age-classes make to population growth. During periods of growth 2-yr-old worms make the greatest contribution, older age-classes during declines, while younger age classes become important during recovery from disturbance. These differences result from temporal and spatial fluctuations in recruitment, individual growth and reproductive activity. Responses of long-lived marine infauna to disturbance likely depend on their current demographic state at the time of disturbance (reflecting demographic conditions such as size/age structure) and factors external to the population (e.g. environmental influences on settlement and recruitment or the type of disturbance). In this case, the disposal of contaminated dredge material had a negative impact on vital rates and potential population growth of *N. incisa* at and 200 m away from the disposal site, but little or no effect on populations 400 m to 3 km away.

## INTRODUCTION

As in many habitats (Pickett & White 1985), disturbance has a major influence on the structure and dynamics of soft-bottom communities (e.g. Boesch et al. 1976, McCall 1978, Pearson & Rosenberg 1978, Woodin 1981, VanBlaricom 1982, Dobbs & Vozarik 1983). Johnson's (1973) 'temporal mosaic' model concisely depicts infaunal communities as collections of patches at different stages of succession. Such successional mosaics are common, being generated by the interplay between forces of disturbance and the ecology of the resident and/or recolonizing species (Whittaker & Levin 1977, Paine & Levin 1981, Sousa 1984, Shugart & Seagle 1985). A key subset of this interplay involves species life histories (e.g. Paine 1979, Whittaker & Goodman

1979, Sousa 1980, Cockburn et al. 1981, Thompson 1985). In this regard, marine infauna are generally seen as falling along a continuum bounded by opportunistic, or weed species adapted to frequent disturbances and 'equilibrium' (or climax) species which are not (Grassle & Grassle 1974, McCall 1977, Rhoads et al. 1978). [We use the terms 'opportunist' and 'equilibrium' as a convenient shorthand for species with particular sets of life history attributes, without reference to factors which promote the evolution or maintenance of such traits.] Opportunists typically are small, tubiculous deposit-feeders (often surface feeders) with short life spans (months) and generation times, and semi-continuous reproduction. They usually respond quickly after disturbance in relatively high numbers, dominate early seral stages and subsequently experience high mortal-

ity (e.g. Grassle & Grassle 1974, McCall 1977; but see Zajac & Whitlatch 1982a,b, Whitlatch & Zajac 1985). Equilibrium infaunal species are generally large, mobile or discretely mobile deposit feeders, or suspension feeders, with longer life spans (years), slow development times and fewer reproductions per unit time. Considered to comprise the climax stage of infaunal succession in coastal habitats (Pearson & Rosenberg 1978, Rhoads et al. 1978, Rhoads & Boyer 1982), they respond slowly after a disturbance, but eventually re-establish their dominant position in the community. This paper centers on the demography of the polychaete *Nephtys incisa*, which has been characterized as an equilibrium species (McCall 1977, Rhoads et al. 1978).

The demography of infaunal field populations is not well known (Brousseau 1978, Weinberg 1985, Zajac 1985, Weinberg et al. 1986, Malinowski & Whitlatch 1988), and few laboratory populations have been studied in this regard (Doyle & Hunte 1981, Åkesson 1982, Gentile et al. 1982, Redman 1985, Levin et al. 1987, Pesch et al. 1987, Whitlatch & Schwartz pers. comm.). For polychaetes, these have centered on primarily opportunistic species. While a number of studies have investigated the population ecology of polychaetes which could be characterized as equilibrium species (e.g. Olive 1977, Beukema & de Vlas 1979, de Wilde & Berghuis 1979, Creaser & Clifford 1982, Heffernan et al. 1983, Valderhaug 1985, Peckol & Baxter 1986), to our knowledge, no attempts have been made to use such information in a demographic framework which lends itself to analyses based on population projection models (e.g. van Groenendael et al. 1988). In this study, estimates of age-specific survivorship and fecundity in a population of *Nephtys incisa* were made and used as inputs for population projection models. These models were analyzed to determine how natural population-level variation shapes this polychaete's demographic characteristics, and how these may be altered by disturbance.

#### Ecology and life cycle of *Nephtys incisa*

*Nephtys incisa* is common to coastal soft-bottom habitats of the northwest Atlantic Ocean (Pettibone 1963), and often dominates (numerically and in biomass) infaunal communities in southern New England waters (Sanders 1956, 1960, Carey 1962, McCall 1977, 1978, Yingst & Rhoads 1978). It burrows in the upper 10 cm of the sediments, ingesting sediments and small infauna (Sanders 1960, Davis 1979). Adults reach a maximum size of ca 10 cm in length.

The early stages of the life cycle are not well known. Adults of congeners shed gametes onto the sediment

surface and water column where fertilization takes place (Bentley et al. 1984). It is not known how long the planktotrophic larvae are in the water column before settlement. Sexual maturity occurs at 1 to 1.5 yr of age and populations are comprised of 3 to 5 year-classes. Each year-class usually consists of 2 cohorts since larvae are produced biannually (Carey 1962, Zajac & Whitlatch 1988). In Long Island Sound, population structure, individual growth rates within a cohort and egg production vary significantly on a spatial and temporal basis (Zajac & Whitlatch 1988).

#### METHODS

**Field site, sampling and data collection.** The field site was located in central Long Island Sound at depths of 15 to 20 m, ca 10 km south of New Haven, Connecticut, USA (Fig. 1). This study is based on infaunal samples taken during the Field Verification Program (FVP) conducted jointly by the US Army Corps of Engineers (ACE) and US Environmental Protection Agencies (EPA). The FVP comprised concurrent measurements of physical and biological processes prior to and following dredge material disposal at a portion of the field site, and laboratory testing of biotic responses to an array of dredge material characteristics (e.g. Gentile et al. 1985, Johns et al. 1985). Prior to disposal operations, 4 stations on an east-west transect, delimiting a gradient of decreasing potential exposure of resident fauna to disposed material, were selected by the

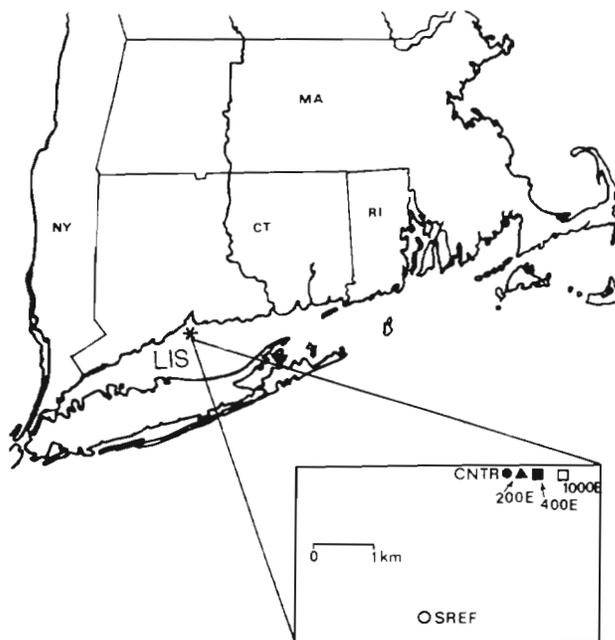


Fig. 1. Location of FVP study site in central Long Island Sound (LIS), USA. Enlargement shows locations of sampling stations at the study site

ACE and EPA. These comprised a station at the center of the disposal area (CNTR) and stations 200, 400 and 1000 m east of the CNTR station (Fig. 1), referred to hereafter as 200E, 400E and 1000E respectively. A fifth sampling station was located ca 3 km south of the CNTR to 1000E transect and designated as a reference site (SREF).

Starting in May 1982, quarterly sets of 5 replicate 0.1 m<sup>2</sup> Smith-McIntyre grab samples were taken at each station. Pre-disposal samples, which were used to assess natural demographic fluctuations in *Nephtys incisa*, were taken in May, August and December 1982 and March 1983. Disposal operations took place between April and May 1983. Approximately 55 000 m<sup>3</sup> of contaminated (oil, grease, metals, PCBs) sediments dredged from Black Rock Harbor, a small inlet located west of Bridgeport, Connecticut, were disposed at CNTR resulting in an almost complete loss of the resident infauna. Details of pre- and post-disposal sediment characteristics, disposal operations and benthic community structure at the FVP site are given by Tomey (1982), Morton (1983) and Germano & Rhoads (1984). Post-disposal samples were taken in June, September and December 1983, and in March and June 1984. (We use pre- and post-disposal to identify these 2 periods of the study with no implication that all stations were affected by disturbance in the latter period.) *N. incisa* population data (abundance, size-structure, reproductive activity) were obtained from 3 to 5 of the replicate grab samples taken at each station for each date and are detailed in Zajac & Whitlatch (1988).

**Demography.** Populations of *Nephtys incisa* in Long Island Sound can have 2 recruitment periods each year

with larvae settling sometime during the spring/summer and fall/winter. Thus, each age-class (year-class) potentially consists of 2 cohorts ca 6 mo apart in age. Eight cohorts (Table 1) were distinguished which settled either prior to (Cohorts A to E) or during (Cohorts X to Z) the 25 mo study period (Zajac & Whitlatch 1988). Cohorts were resolved from overall size-frequency distributions for each station at each sampling period using statistical analyses of distribution mixtures (Macdonald & Pitcher 1979, Macdonald & Green 1985), and ages assigned based on growth data and analyses of rings in the teeth of *N. incisa* (Zajac & Whitlatch 1988). Survivorship and fecundity were calculated using data obtained from analyses of cohort distribution mixtures which yielded estimates of the proportion of each cohort in the population,  $\pi$ , and mean individual size within a cohort,  $S$ . Demographic models were based on the flow of cohorts through age-classes (0-yr-old larvae to adults 4+ yr of age) over the course of the study.

**Cohort survivorship:** Survivorship estimates were based on changes in cohort-specific density. For each station, the density (per 0.1 m<sup>2</sup>) of Cohort  $i$ ,  $D_{it}$ , at time  $t$  was calculated by:

$$D_{it} = \frac{\pi_{i1} N_t}{n_t} \quad (1)$$

where  $N_t$  = total number of individuals in the sample at  $t$ ; and  $n_t$  = number of replicate samples. Survivorship to each sampling date,  $l_t$ , was then calculated by dividing each density value by a cohort's density in May 1982 or when it first appeared in the samples. In a few cases, the density of a cohort increased from one time to the next, yielding increasing  $l_t$  values. These departures

Table 1. *Nephtys incisa*. Ages of cohorts at the FVP study site in central Long Island Sound between May 1982 and June 1984, and their assignment to yearly age-classes. Cohorts are designated by A, B, C etc. Cohorts with no lines under their age represent juveniles < 1 yr old, 1 line = 1-yr-old adults (A1), 2 lines = 2-yr-old adults (A2), 3 lines = 3-yr-old adults (A3), 4 lines = 4-yr-old adults (A4). See text for details

Date	Cohort							
	X	Y	Z	A	B	C	D	E
May 1982	—	—	—	3 mo	9 mo	<u>1-2 yr</u>	<u>2-3 yr</u>	<u>4 yr</u>
August	—	—	—	6 mo	<u>1 yr</u>	=====	=====	=====
December	—	—	3 mo	10 mo	<u>1-4 mo<sup>a</sup></u>	<u>2-3 yr</u>	<u>3-4 yr</u>	<u>4 +</u>
March 1983	—	—	6 mo	<u>1-1 mo</u>	<u>1-7 mo</u>	=====	=====	=====
June	—	—	9 mo	<u>1-4 mo</u>	<u>1-10 mo</u>	=====	=====	=====
September	—	3 mo	<u>1 yr</u>	<u>1-7 mo</u>	<u>2-1 mo</u>	<u>3-4 yr</u>	<u>4 +</u>	=====
December	—	6 mo	<u>1-3 mo</u>	<u>1-10 mo</u>	<u>2-4 mo</u>	=====	=====	=====
March 1984	1 mo	9 mo	<u>1-6 mo</u>	<u>2-1 mo</u>	<u>2-7 mo</u>	=====	=====	=====
June	4 mo	<u>1 yr</u>	<u>1-9 mo</u>	<u>2-4 mo</u>	<u>2-10 mo</u>	=====	=====	=====

<sup>a</sup> Read as 1 yr, 4 mo old

were not great (Zajac & Whitlatch 1987) and, for subsequent analyses,  $l_t$  values were smoothed by rounding to the closest integer value which did not produce an increase.

**Fecundity and larval production:** Individual fecundity,  $F$ , was estimated using an allometric relationship between female worm size and egg number:

$$\log F = 3.01 (\log W) + 2.46 \quad (2)$$

( $R^2 = 0.8237$ ,  $p < 0.0001$ ,  $N = 43$ ), where  $W$  = width of the 10th segment in mm (Zajac & Whitlatch 1988). Changes in fecundity were tracked by calculating an age-specific value,  $F_x$ , at each sampling date using individual mean size in the cohort,  $S$ , which entered a particular age-class on that date (see below).  $F_x$  values were divided by 2 to reflect the production of female offspring only. Temporal fluctuations in potential, total larval production by each age-class were estimated by multiplying  $F_x$  values by the mean density of adults in that age-class in the population at each sampling time.

**Structure of the demographic models and analyses:** To examine demographic characteristics and dynamics of *Nephtys incisa*, station-specific population projection models (Leslie 1945) were generated for pre- and post-disposal periods. In the models, populations were structured by age. Age-classes consisted of juveniles (J) less than 1 yr old, and 4 adult groups ranging from 2 to 4+ yr of age (A1 to A4, respectively; see Table 3).

Our models depict yearly demographic changes in the populations. However, since there are 2 recruitment periods per year, we initially calculated age-specific vital rates based on cohort survivorship over half-year intervals. For the pre-disposal period, survivorship probabilities were estimated by tracking each cohort between May and December 1982 and between December 1982 and March 1983. Since the sampling date 6 mo after December 1982 was June 1983, which was just after dredge material disposal, we felt that using March 1983 samples would be more representative of pre-disposal dynamics. Post-disposal half-year transitions were based on changes occurring between March and September 1983, and September 1983 and March 1984.

Post-settlement  $l_t$  values were used to estimate the probability of survivorship from one age-class to the next over half-year increments (except for larval survivorship) by:

$$P_x = l_t/l_{t-1} \quad (3)$$

where  $P_x$  = probability of survivorship to age  $x$  from age  $x-1$ , with  $l_t$  values corresponding to cohorts attaining a particular age  $x$  at time  $t$ . These half-year, cohort-specific survivorship values were then averaged to obtain a yearly, age-class specific  $P_x$  value.

Larvae to juvenile  $P_x$  (i.e.  $P_0$ ) values were calculated

on a site-specific basis by dividing the density of new recruits in the population at the beginning of each half-year by the estimated total larval production of the population from the previous period. For example, values for the pre-disposal May to December 1982 transition were calculated by dividing the mean number of Z cohort individuals found in December 1982 at each site by the total larval production estimated for the previous May. For pre-disposal population models, an additional estimate of larval survivorship was made. There was no indication of recruitment in March 1983 at any of the stations (Zajac & Whitlatch 1988), thus larval survivorship was effectively zero. Since our intent was to produce a 'baseline' demographic model for *Nephtys incisa* using the pre-disposal data, we included an estimate of larval survivorship that reflected conditions when recruitment was high, as occurred upon recruitment of Cohort A (see Table 1) into the population sometime prior to the initial May 1982 samples. We estimated larval survivorship under these conditions by dividing the number of Cohort A individuals found in May 1982 by the total larval output estimated for December 1982. This value was then averaged with the other larval survivorship values obtained to produce the values given in the pre-disposal matrices.

Larval survivorship calculated for infauna with planktonic larvae, such as *Nephtys* spp., can lead to uncertain estimates of population growth, since local recruitment may be related to the dynamics of distant populations in addition to local populations (Ayal & Safriel 1982). Depending on the extent of mixing and dispersal due to current regimes and weather conditions, it may not be possible to discriminate survivorship probabilities of larvae produced by particular populations. We acknowledge this potential source of error, but feel that when comparing a number of populations as we have done in this study, our method of estimating larval survivorship is a valid first order approximation. The estimates did not depend on age-specific fecundities of populations for the time vital rates were being estimated (except in the one case noted above), but rather on the fecundity and density of the reproductive adults during the previous time period. Our estimates reflect the contribution of each site to the total pool and the net return based on that contribution, yielding a station-specific estimate of larval survivorship for a portion of a larger and admittedly interacting population.

Fecundity estimates were based on December 1982, March and September 1983, and March 1984 worm sizes. For age-specific fecundity,  $F_x$ , half-year, cohort-specific values for A1 and A2 age-classes were added to reflect that these females can reproduce twice in one year. For females  $> 3$  yr old, half-year  $F_x$

values were averaged since it appears these generally produce only one batch of gametes per year (Zajac & Whitlatch 1988). Age-specific  $F_x$  values were multiplied by site-specific  $P_0$  values and estimated survivorship of settled juveniles prior to 1 yr of age to yield effective fecundity values used in the population matrices. Also, when larval survivorship fell to zero due to the absence of recruitment during several seasons of observation (Zajac & Whitlatch 1988), we assumed adults did spawn during these periods but larvae did not survive to settlement. It is possible, however, that adults reabsorbed their gametes and did not spawn.

Population matrices were solved for  $\lambda$  (the dominant eigenvalue of the matrix), which we interpret as the potential population growth rate (Bierzychudek 1982, Zajac 1985).  $\lambda$  is equal to  $e^r$  where  $r$  is the intrinsic rate of increase in a population. When  $\lambda = 1$ ,  $r = 0$  and population size remains stable; values of  $\lambda$  above 1 indicate increasing population size, values below 1 decreasing population size. Several other demographic characteristics were calculated: (a) age-specific reproductive value (RV), the expected reproductive contribution of an  $x$ -aged individual to population growth (e.g. Charlesworth 1980, Caswell 1982), (b) the sensitivity of  $\lambda$  to changes in vital rates (Caswell 1978), and (c) elasticity (de Kroon et al. 1986), which

estimates proportional sensitivities and the relative contributions of vital rates to population growth. Analytical formulae for these demographic characteristics can be found in the cited references (also see van Groenendael et al. 1988).

## RESULTS

### Survivorship, fecundity and larval production

Survivorship patterns differed between sites for individual cohorts (Fig. 2). Survivorship at CNTR went to zero for each cohort during disposal operations (March to June 1983). However, individuals in Cohorts A, B and Z were found at CNTR by September 1983. Thus, the overall post-disposal 'survivorship' patterns for these cohorts at CNTR reflect mortality and migration; for statistical and demographic analyses the mean number of individuals in June 1983 was set to the value obtained for the following sampling date after migration onto the dump site.

Station differences in survivorship were statistically significant for Cohorts A, B and C (Table 2). Examination of the test statistic components reveals that for Cohort A almost all of the contribution to the significance was due to low survivorship at CNTR following

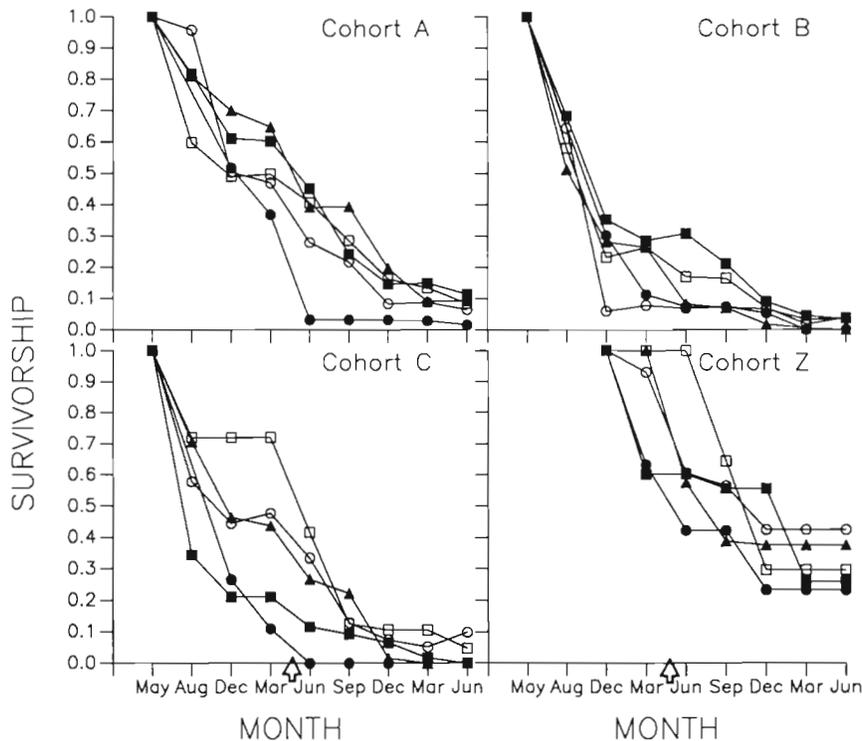


Fig. 2. *Nephtys incisa*. Survivorship of most abundant cohorts found during the study at each station. Arrows indicate point at which dredged sediments were disposed at the CNTR station. Starting ages of cohorts are given in Table 1. Station symbols as in Fig. 1

Table 2. *Nephtys incisa*. Results of statistical analyses of between station differences in cohort survivorship over the study period at the FVP study site in central Long Island Sound. Starting ages of each cohort given in Table 1. Values used in the test are those shown in Fig. 3. Tests were done using Peto & Peto's (1972) logrank method given in Pyke & Thompson (1986). LR is the logrank statistic which was compared to critical values of  $\chi^2$  with 4 degrees of freedom. Station-specific contributions to LR are given under station headings

Cohort	LR	Test	SREF	1000E	400E	200E	CNTR
A	29.23	$p < 0.001$	0.781	0.001	1.041	2.092	25.31
B	10.69	$p < 0.05$	6.994	0.000	3.061	0.343	0.292
C	8.59	$0.10 > p > 0.05$	1.249	1.060	2.813	0.420	3.049
D	2.20	$0.90 > p > 0.50$	0.781	0.142	0.053	0.800	0.425
Z	5.98	$0.50 > p > 0.10$	0.610	1.020	0.708	0.961	2.678

disposal. Component values were also slightly higher at 200E and 400E than at SREF and 1000E. For Cohort B, most of the significance was due to low survivorship at SREF and relatively high survivorship at 400E. Among-station differences for Cohort C were marginal, but the analyses suggest that the patterns differed primarily at CNTR and 400E. At both of these stations, pre-disposal survivorship was low, while following disposal no Cohort C individuals were found migrating to (surviving at) CNTR. The loss of Cohort C individuals from the overall population occurred first at CNTR (September 1983) followed by 200E (December 1983), 400E (March 1984) and 1000E (June 1984). At SREF, Cohort C individuals were still present in the population at the end of the study period. Cohort B had also effectively died out of the population at CNTR and 200E by March 1984 while persisting at the other stations (Fig. 2).

To provide information on variation in survivorship to

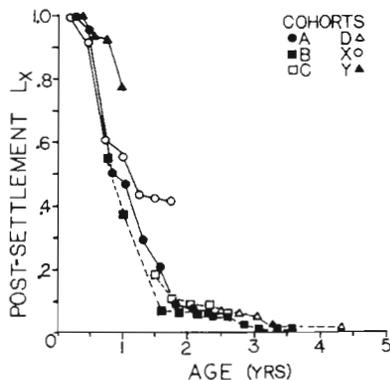


Fig. 3. *Nephtys incisa*. Composite post-settlement survivorship curve based on cohort data from SREF. Cohorts A, Z and Y were newly recruited worms and survivorship was initially set to 1.0. For other cohorts, initial survivorship values were interpolated based on values obtained for younger cohorts. For example Cohort B's initial value was set to 0.55 based on values of 0.6 and 0.5 for Cohorts X and A, respectively. Subsequent values were calculated using this initial estimate and values given in Fig. 2 and Zajac & Whitlatch (1987). Since few individuals of Cohort Y were found, values given in the graph are averages based on data from all 5 stations

particular ages,  $l_x$ , a composite post-settlement survivorship curve based on cohorts at SREF was constructed (Fig. 3). It is apparent that among-cohort  $l_x$  variation was greater in worms  $< 2$  yr old. Cohorts Z and Y which settled during the study period had higher survivorship between 3 and 20 mo of age than Cohorts A and B, but values for Cohorts A, B, C and D were similar for worms  $> 2$  yr old.

Fecundity varied over 2 orders of magnitude between age-classes, increasing sharply in females 2 yr old and greater (Fig. 4). In general, age-specific fecundities were similar between stations and over most of the study period. Much of the variation was related to older, larger females dying out in the populations and new individuals entering older age-classes being smaller in size (Zajac & Whitlatch 1988). This was especially evident when Cohort B entered the A1 age-class in December 1982 and the A2 age-class in September 1983. Decreases in A1 and especially A2 fecundity at 200E and CNTR throughout the post-disposal period resulted from decreases in growth following disposal (Zajac & Whitlatch 1988). The lowest age-specific fecundities in September 1983 were found at CNTR and 200E, perhaps due to a combination of cohort changeover in the age-classes and disposal effects on growth.

The contribution each age-class made to total larval production was not directly related to age (and size) but varied depending on  $F_x$  and the number of x-yr-olds present in the population (Fig. 5). Prior to disposal, younger age-classes (A1 and A2) potentially produced greater or equal numbers of larvae relative to older worms due to their higher abundances (Zajac & Whitlatch 1988). Following disposal, differences between age-classes became more pronounced. At 1000E and 400E, A1 contributions to total larval production fell off relative to older age-classes (after September 1983) but overall production remained high. Larval production decreased in general during this period at 200E and CNTR reflecting the loss of older individuals in these populations. Also, few A1 individuals were reproductive at CNTR during the post-disposal period. In June

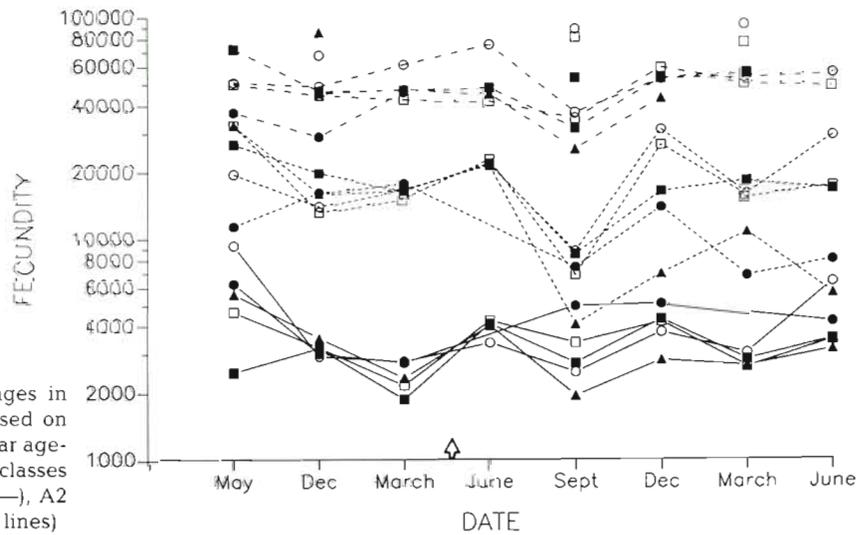


Fig. 4. *Nephtys incisa*. Age-specific changes in fecundity ( $F_x$ ) during the study period based on mean size of individuals entering a particular age-class. Station symbols as in Fig. 1. Age-classes from bottom grouping of values are A1 (—), A2 (.....), A3 (---), and A4 (no connecting lines)

1983, there was no larval production at CNTR due to loss of all individuals and lack of immigration.

#### Population growth and reproductive values

Pre- and post-disposal population matrices, derived from the survivorship and fecundity results presented above, are shown in Table 3. Age-class composition varied between sites during the study. Prior to disposal, worms 4+ yr old were found at SREF and 200E but not at 1000E, 400E and CNTR. Following disposal, A4 individuals were present at SREF, 1000E and 400E, but not at 200E and CNTR. At the latter 2 stations the maximum age attained following disposal was 3 and 2 yr, respectively. While age-specific  $P_x$  transitions varied in no definite pattern, apart from times when values fell to zero for the oldest age-classes, age-specific effective fecundities dropped sharply in the second year due to decreases in larval survivorship (Table 3).

Analyses of pre-disposal matrix models yielded positive  $\lambda$  values for each station (Table 4), suggesting a potential for population increase. In contrast, post-disposal models yielded reductions in  $\lambda$  at each station, below population maintenance levels, notably at 200E and CNTR.

Pre-disposal reproductive value (RV) increased with age up to A2 individuals at each station, but diverged for older females (Fig. 6). At 200E and SREF, RVs peaked in the A3 age-class and declined with age at the other stations. Post-disposal RV patterns were more variable among stations. At SREF, 1000E and 400E the RV of all age-classes was similar, although they slightly increased (SREF) or decreased (400E) with age. In contrast, RV dropped off sharply from peak juvenile values through all age-classes at CNTR, while at 200E values leveled off in adult age-classes.

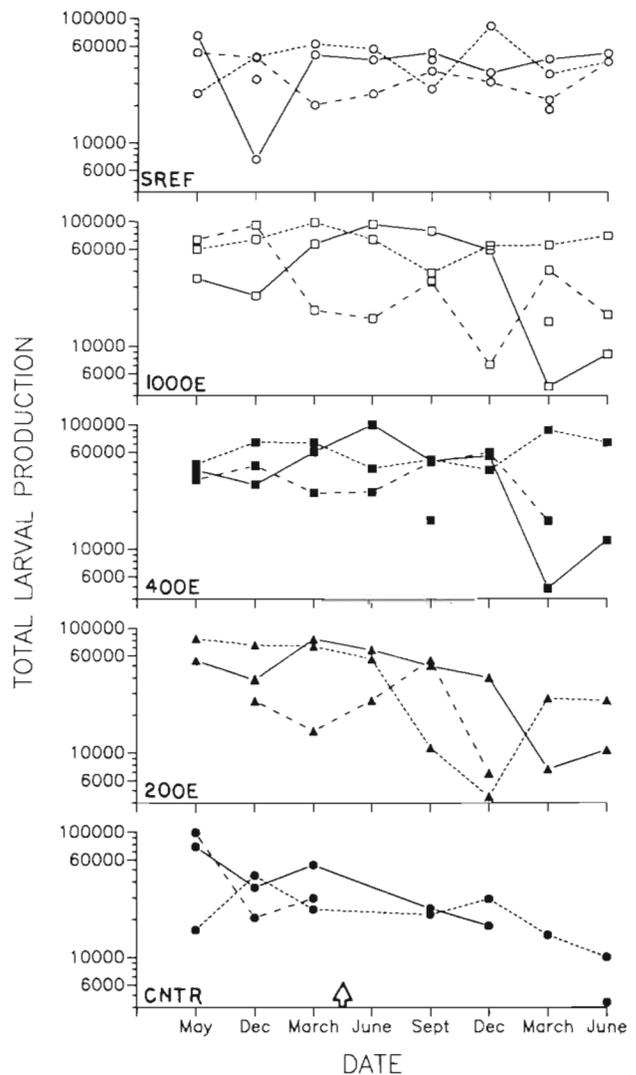


Fig. 5. *Nephtys incisa*. Age-specific contributions to total larval production in populations at each FVP station. Station symbols and age-class designations as in Fig. 4

Table 3. *Nephtys incisa*. Pre- and post-disposal population matrix values at each FVP station. Post-disposal vital rates are given in parentheses. Age-classes J through A4 are explained in 'Methods' A dash indicates a zero entry in the matrix. Larval/juvenile survivorship values used to calculate effective fecundity are given next to station heading

SREF $0.123 \times 10^{-3}$ ( $0.125 \times 10^{-4}$ )					
	J	A1	A2	A3	A4
J	-	0.699 (0.068)	3.754 (0.307)	6.747 (0.571)	4.414 (1.130)
A1	0.505 (0.656)	-	-	-	-
A2	-	0.723 (0.682)	-	-	-
A3	-	-	0.553 (0.366)	-	-
A4	-	-	-	0.229 (0.453)	-
1000E $0.828 \times 10^{-4}$ ( $0.370 \times 10^{-5}$ )					
	J	A1	A2	A3	A4
J	-	0.441 (0.023)	2.335 (0.041)	3.582 (0.157)	- (0.289)
A1	0.616 (0.577)	-	-	-	-
A2	-	0.720 (0.457)	-	-	-
A3	-	-	0.502 (0.511)	-	-
A4	-	-	-	- (0.699)	-
400E $0.790 \times 10^{-4}$ ( $0.581 \times 10^{-5}$ )					
	J	A1	A2	A3	A4
J	-	0.399 (0.032)	2.852 (0.156)	3.767 (0.254)	- (0.155)
A1	0.626 (0.564)	-	-	-	-
A2	-	0.606 (0.575)	-	-	-
A3	-	-	0.607 (0.274)	-	-
A4	-	-	-	- (0.267)	-
200E $0.927 \times 10^{-4}$ ( $0.881 \times 10^{-5}$ )					
	J	A1	A2	A3	A4
J	-	0.542 (0.040)	3.005 (0.130)	4.275 (0.111)	3.958
A1	0.607 (0.749)	-	-	-	-
A2	-	0.703 (0.209)	-	-	-
A3	-	-	0.390 (0.254)	-	-
A4	-	-	-	0.200	-

Table 3 continued

CNTR $0.148 \times 10^{-3}$ ( $0.583 \times 10^{-5}$ )					
	J	A1	A2	A3	A4
J	-	0.845 (0.029)	4.996 (0.081)	5.527	-
A1	0.423 (0.614)	-	-	-	-
A2	-	0.556 (0.554)	-	-	-
A3	-	-	0.696	-	-
A4	-	-	-	-	-

Table 4. *Nephtys incisa*. Potential population growth rates,  $\lambda$ , in central Long Island Sound calculated from pre- and post-disposal population matrices given in Table 3

Station	Pre-disposal $\lambda$	Post-disposal $\lambda$	% Change
SREF	1.431	0.760	-52.4
1000E	1.262	0.535	-57.4
400E	1.273	0.494	-63.5
200E	1.326	0.351	-74.9
CNTR	1.185	0.332	-76.4

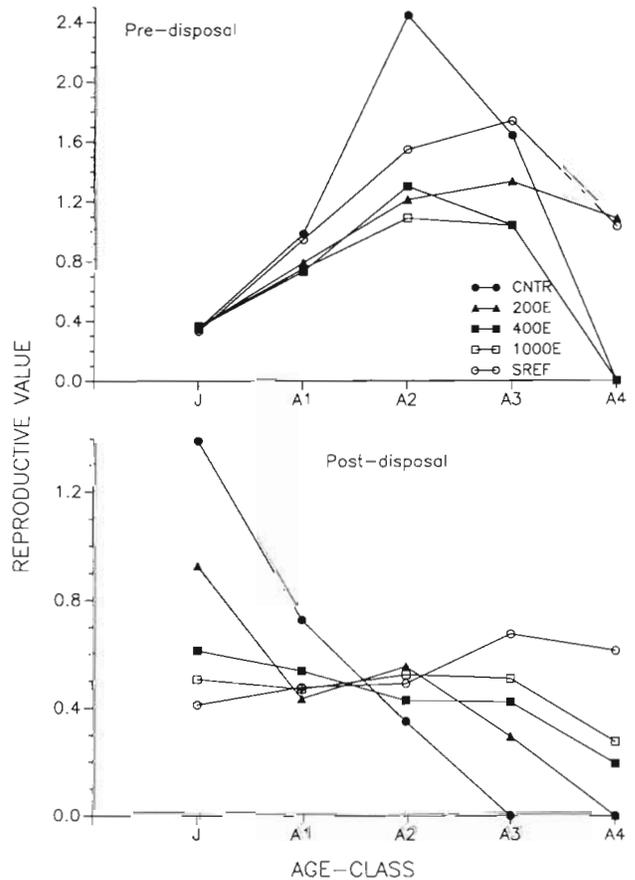


Fig. 6. *Nephtys incisa*. Age-specific changes in reproductive value in pre- and post-disposal populations in central Long Island Sound. Age-classes as defined in the text

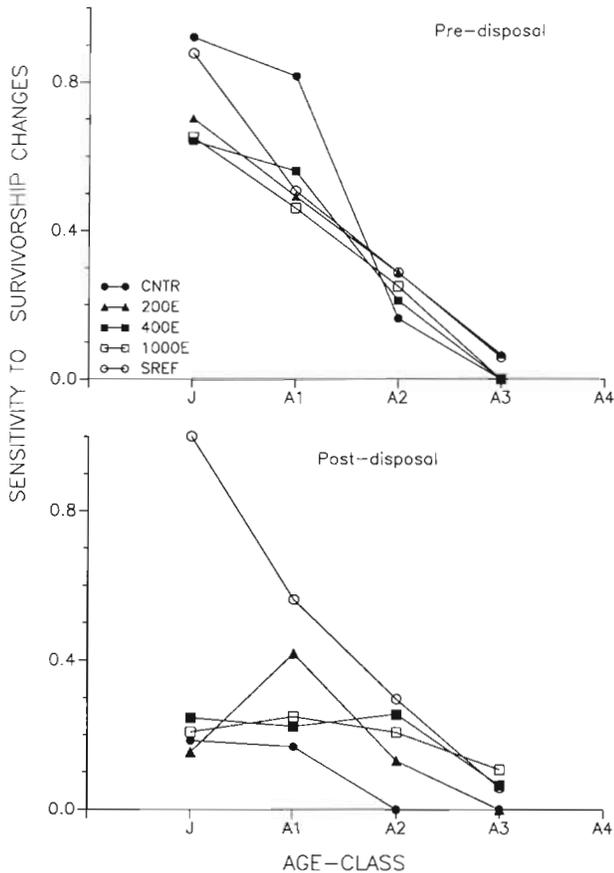


Fig. 7. *Nephtys incisa*. Sensitivity of population growth to age-specific changes in survivorship,  $P_x$ , during pre- and post-disposal periods in central Long Island Sound. Age-classes as defined in the text

#### Sensitivity and elasticity

For pre-disposal models, age-specific sensitivity of  $\lambda$  to changes in survivorship was similar among stations; pronounced among-station differences were evident following dredge disposal (Fig. 7). Prior to disposal,  $\lambda$  was most sensitive to changes in the survivorship of juveniles to adults, and declined steadily for subsequent age-classes. Following disposal, there was a similar pattern at SREF. At 1000E, 400E and CNTR survivorship sensitivity was nearly constant over all age-classes, but at 200E there was a sharp increase in the sensitivity of the transition from A1 to A2 adults.

Among-station differences in the sensitivity of  $\lambda$  to changes in age-specific fecundity were similar to those for survivorship (Fig. 8). Pre-disposal values for each station were nearly identical, declining steadily with age. After disposal, fecundity sensitivity was relatively constant over juvenile and most adult ages at SREF, 1000E and 400E. At CNTR and 200E there were sharp increases in the A1 and A2 age-classes.

Pre-disposal, station-specific elasticity patterns for *Nephtys incisa* were nearly identical (Fig. 9). Elasticities

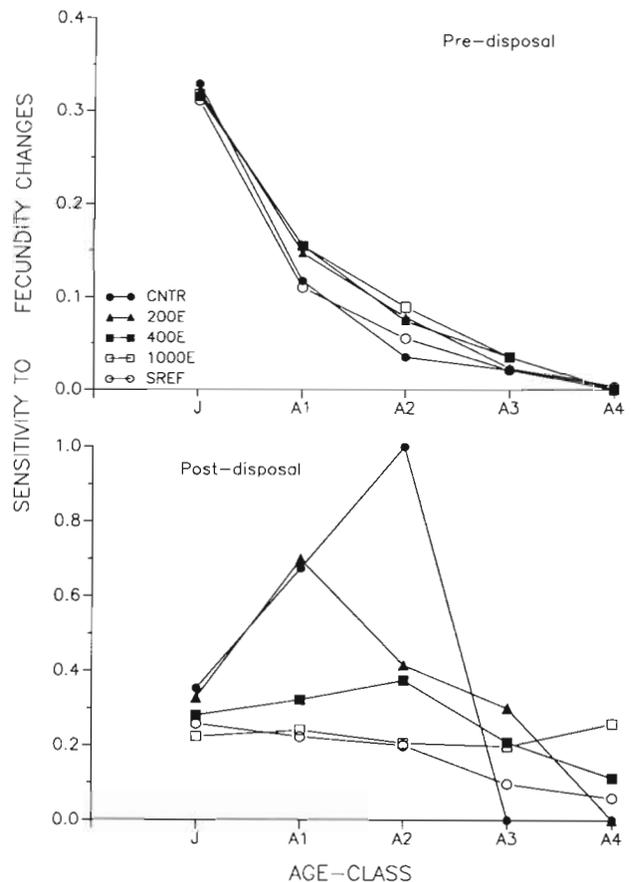


Fig. 8. *Nephtys incisa*. Sensitivity of population growth to age-specific changes in fecundity,  $F_x$ , during pre- and post-disposal periods in central Long Island Sound. Age-classes as defined in the text

of transitions to A1 and A2 age-classes were higher than for other portions of the life cycle. A1 and A2  $F_x$  elasticities always fell below  $P_x$  values for these age-classes, but A3 and A4  $P_x$  and  $F_x$  elasticities were similar. Elasticity patterns changed during the post-disposal period. At SREF, 1000E and 400E,  $P_x$  elasticities for A1 and A2 transitions fell below pre-disposal values, but were higher for subsequent transitions.  $F_x$  elasticities were lower than  $P_x$  values in all cases except for the terminal age-class. Elasticity patterns at CNTR and 200E differed from the other 3 stations during this period. At 200E,  $P_x$  values were identical to pre-disposal values;  $F_x$  elasticities showed maxima in A2 age-class. At CNTR, A1 and A2  $P_x$  elasticities were higher than pre-disposal values and A2  $F_x$  elasticity rose sharply from a low A1 value.

#### DISCUSSION

##### Natural demographic variation and population growth

Populations of *Nephtys incisa* in central Long Island Sound exhibited several demographic states during the

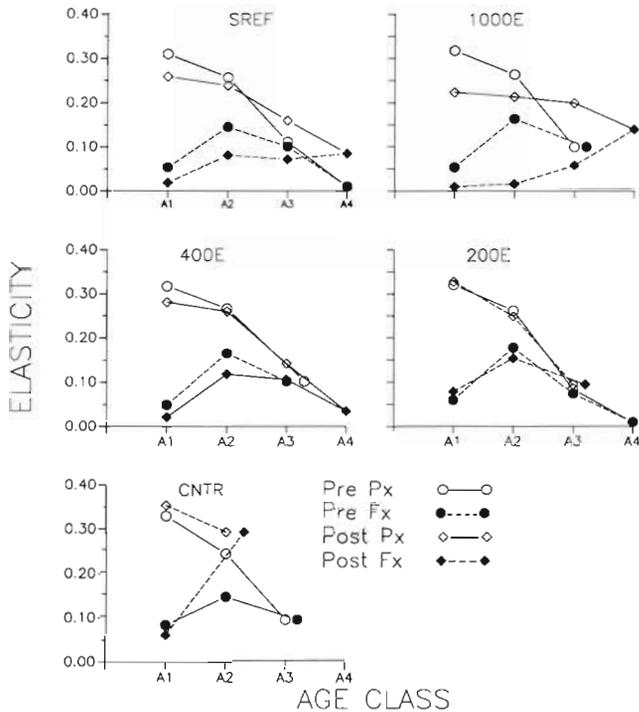


Fig. 9. *Nephtys incisa*. Age-specific elasticity (proportional sensitivity and transition contributions to population growth) values for pre- and post-disposal populations.  $P_x$  symbols denote elasticities for survivorship transitions from one age-class to the next;  $F_x$  symbols denote elasticities for age-specific fecundities. Age-classes as defined in the text

study period related to natural fluctuations in population dynamics. Between May 1982 and March 1983 (the pre-disposal period), a number of factors combined to yield positive population growth rates at each station (Table 4). Primary among these were relatively strong recruitment pulses both just prior to the initiation of the study, in the case of Cohorts A and B, and, to a lesser extent, in the case of Cohort Z during the pre-disposal period (Zajac & Whitlatch 1988). These resulted in larval survivorship estimates that were 1 to 2 orders of magnitude higher than those estimated for the post-disposal period. Since age-specific fecundities did not appear to change to any great extent between the 2 periods, high larval survivorship was the key factor determining pre-disposal effective fecundities which were an order of magnitude higher than those following disturbance. Secondly, age-specific survivorship,  $P_x$ , also tended to be 6 to 10 % higher for younger, and 33 to 70 % higher for older age-classes during the first year. During the second year of the study (June 1983 to 1984, the post-disposal period), effective fecundity as well as survivorship to most age-classes decreased, resulting in negative population growth rates at all stations.

Concomitant with these demographic changes were changes in population structure. During the pre-dis-

posal phase, populations were dominated by juveniles and young adults (primarily Cohorts A, B and C), and adults were somewhat larger in size relative to individuals of subsequent cohorts entering these age-classes (Zajac & Whitlatch 1988). Following disposal, populations became progressively adult-dominated due to an almost complete lack of recruitment, and adults were generally smaller in size.

Consideration of the reproductive value, sensitivity and elasticity analyses provides insights into the impact different age-classes can have a population growth during varying environmental and demographic conditions (de Kroon et al. 1986, van Groenendael et al. 1988). While there was some variation between stations (Fig. 6), RV patterns indicate that during periods of population increase female reproductive contributions to population growth are greatest at 2 and 3 yr of age. This is also supported by our estimates of total larval production showing that the A2 age-class frequently contributed equivalent or the most number of larvae to the overall larval pool relative to other age-classes (Fig. 5). These worms are also more likely to produce 2 broods in 1 yr (Zajac and Whitlatch 1988). In populations where cohorts survive to the A4 class, females potentially make increasingly greater or similar reproductive contributions. However, the actual numbers of larvae produced by older worms may fall below younger age-classes depending on their relative densities. In contrast, RVs were similar over all age-classes during the second year of the study (excluding juvenile values at 200E and CNTR), suggesting that during periods of population decline all age-classes make equivalent reproductive contributions to further population growth.

Sensitivity analyses indicated that on an overall basis, changes in survivorship and fecundity during a period of population increase would have decreasing impacts on  $\lambda$  with age, and that survivorship sensitivities were higher than those for fecundity (Figs. 7 and 8). This pattern is common for populations which have positive values of  $\lambda$  (Caswell 1978, Levin et al. 1987). For both survivorship and fecundity, post-disposal models yielded more variable among-station sensitivity patterns, and more constant values over much of the life history of *Nephtys incisa*. It appears then that as populations of *N. incisa* shift to a decline phase, demographic changes in older age-classes would have equivalent or greater impacts on  $\lambda$  as opposed to rapidly decreasing impacts under conditions of population growth. Also, fecundity and survivorship sensitivities become of equal magnitude during population decline periods.

Elasticity patterns indicate that on a relative basis, the critical demographic factor in terms of age-class contributions to  $\lambda$  is survivorship. In all cases survivorship elasticities exceeded fecundity values, except in the terminal age-class, especially through A1 and A2

age-classes. However, during the second year, elasticity patterns indicated that survivorship through later adult ages (A3 and A4) made increasing contributions to  $\lambda$ , similar to the results of the sensitivity analyses.

As in other nephtyid polychaetes (Olive & Morgan 1984), declines in population abundance of *Nephtys incisa* are correlated to periods of recruitment failure. Low to non-existent recruitment was found over much of the study period across the entire FVP site (Zajac & Whitlatch 1988). During periods of strong recruitment, and increasing abundance, younger adults appear to make greater contributions to population growth as suggested by high A2 reproductive values, steady declines in the sensitivity of  $\lambda$  to survivorship and fecundity changes with age, and high A1 and A2 elasticities. However, during periods of recruitment failure, which may last up to 2yr, older adults may be critical in keeping local populations from going extinct. During the second year of this study, RVs of all age-classes were similar (at SREF, 1000E and 400E) as were sensitivities to survivorship and fecundity, and elasticity analyses indicated increasing contributions to  $\lambda$  by older age-classes relative to pre-disposal values. Older worms had more consistent periods of growth (Zajac & Whitlatch 1988), less variable mortality (Fig. 3) and higher fecundity (Fig. 4). Many of these benefits may be due in part from the ability of larger *N. incisa* to retreat deeper into the sediments (Davis 1979), where they would be less prone to various sources of mortality (McCall 1977).

Longevity and high larval production by *Nephtys incisa* may maintain populations during low recruitment periods until changes in local conditions promote successful recruitment. However, it is easy to envisage this situation as unstable if conditions promoting successful spawning and/or recruitment do not occur over the life span of the worms since older worms generally spawn only once a year. Thus, reproductive periodicity for long-lived, polytelic (Olive & Clark 1978) polychaetes is critical to their demographic dynamics. Asynchronous reproductive activity, which was evident between populations at the study site (Zajac & Whitlatch 1988), may act to spread the risk of recruitment failure across time and space. At the population level, asynchronous reproductive activity by subpopulations will result in the release of larvae throughout most of the year increasing the opportunities for successful larval settlement in a heterogeneous environment, depending on the dispersal range of the larvae.

#### Demographic changes following disturbance

Superimposed on this shifting pattern of yearly demographic variation were demographic alterations due to disturbance at CNTR and 200E which resulted

in even greater reductions in  $\lambda$  relative to declines at SREF, 1000E and 400E. Since the CNTR population was extirpated during disposal of dredge materials, our results provide information on the initial demographic recovery of *Nephtys incisa* following disturbance. At CNTR, recolonization was via immigration of 1- and 2-yr-old adults and low level recruitment of juveniles (Zajac & Whitlatch 1988). Demographic conditions which can be attributed to disturbance were low survivorship to the A2 age-class at 200E, and low A2 fecundities at CNTR and 200E due to growth reductions following disturbance (Zajac & Whitlatch 1988). More distinct was the absence of A4 individuals at 200E and A3 and A4 individuals at CNTR after 1 yr of recovery (Table 3). Total larval production also declined at both stations (Fig. 5). Since we have data only on the first year of recovery, we do not know how long it would take CNTR and 200E populations to recover to ambient demographic conditions in the habitat. The absence of older age-classes at these stations suggests recovery may take several years if these worms do not actively migrate. In the absence of storms which can passively redistribute infauna (Dobbs & Vozarik 1983), a full complement of age-classes will only result from aging of younger cohorts and continued recruitment of new cohorts.

The situation in this study is complicated by the nature of the disturbance. Numerical recovery at CNTR (Zajac & Whitlatch 1988) was the lowest found to date for this species in response to disturbance (McCall 1977, Rhoads et al. 1977, 1978). In these other studies disturbed sediments were either defaunated natural sediments or dredged sediments capped with clean sand. The uncapped, contaminated sediments that were disposed at CNTR had negative effects on *Nephtys incisa*'s growth and burrowing activity in the laboratory (Johns et al. 1985). Thus, while the worms present at the most affected stations may make the transition into older age-classes, they may continue to be smaller and/or the toxicity of the sediments may increase their mortality. For example, Johns et al. (1985) found that worms did not burrow as deeply in the disposed sediments. As a result, they may be more prone to total or partial predation. Furthermore, the sediments may prove to be unattractive to settling larvae, and/or reduce the growth of newly settled individuals. These would be critical changes in light of post-disposal demographic changes at CNTR and 200E. Reproductive values were highest in younger age-classes, sensitivity of  $\lambda$  to changes in early  $P_x$  was high at 200E and at CNTR and 200E for early  $F_x$  relative to other stations (Figs. 6 and 7), while  $P_x$  elasticities were of the same magnitude (200E) or increased (CNTR) for young worms (Fig. 8).

Disposal of contaminated sediments in soft-bottom

habitats likely exacerbates more natural demographic responses to disturbance, resulting in extended recovery periods. In this study it appears that recruitment failure and shifts in adult sizes in particular age-classes resulted in 52 to 63 % reductions in  $\lambda$  (Table 4). Disposal activities can be seen as causing an additional ca 20 % decrease in  $\lambda$ , for an overall reduction of 75 % relative to pre-disposal values. However, pre- and post-disposal population models presented here are in all likelihood a subset of the possible demographic states that can occur in this species. Had dredge disposal occurred while populations were in a different demographic state (e.g. akin to the pre-disposal matrix model), or if environmental factors changed some important parameter (e.g. if recruitment was heavy during the post-disposal period), then disturbance effects, as well as subsequent recovery of the affected populations, may have been quite different.

## CONCLUSIONS

As shown in this study, vital rates can vary considerably over time and space in *Nephtys incisa*. However, populations were a relatively coherent demographic unit over the spatial scales (200 m to 3 km) investigated here, apart from the local disturbance effects at 200E and CNTR. Temporal differences were more distinct, revealing fluctuating contributions to population growth between younger and older age-classes. Depending on the disturbance history of the habitat and factors determining recruitment success, the long-term demographic dynamics of *N. incisa* will vary between years in which mid-age adults contribute most to growth and older age-classes to maintaining populations during periods of decline. In portions of habitats recovering from disturbance younger age-classes will make increasing contributions. This makes for a varied selective regime in terms of life history evolution. While life histories of infauna are seen as related to benthic disturbance regimes, the demographic variation exhibited by *N. incisa* suggests that life history traits may be under the evolutionary influence of a suite of factors of which disturbance periodicity and magnitude is but a component. Given the paucity of information on the interplay between disturbance and population-level processes for marine infauna (Guillou & Hily 1983, Levin 1984, Zajac & Whitlatch 1988; also see Zajac & Whitlatch 1985), it is not yet possible to gauge the relative importance of these factors with respect to infaunal successional dynamics, how this relates to the overall population dynamics of species comprising benthic communities, and the evolution of their life histories. As such, we feel that it will be necessary to study more fully the extent of natural demographic

variation in opportunists and equilibrium species and how their demographic dynamics differ, in order to determine how these influence responses to disturbance and successional changes.

*Acknowledgements.* We would like to thank C. Crouch, R. Degoursey, L. Gypson, B. Lussier and E. Wessels for their assistance in various aspects of this study. C. Pesch, G. Pesch, J. Gentile and C. Glorioso of the US EPA greatly facilitated project administration and coordination. This research was funded by the United States Environmental Protection Agency under cooperative agreement CR-811727. It has not been subjected to the Agency's peer and administrative review and therefore may not necessarily reflect the views of the Agency and no official endorsement should be inferred. This is Contribution No. 219 from the Marine Sciences Institute, University of Connecticut.

## LITERATURE CITED

- Åkesson, B. (1982). A life table study on three genetic strains of *Ophryotrocha diadema* (Polychaeta Dorvilleida). *Int. J. Invertebrate Repro.* (Amsterdam) 5: 59–69
- Ayal, Y., Safriel, U. N. (1982). r-Curves and the cost of the planktonic stage. *Am. Nat.* 119: 391–401
- Bentley, M. G., Olive, P. J. W., Garwood, P. R., Wright, N. H. (1984). The spawning and spawning mechanism of *Nephtys caeca* (Fabricius, 1780) and *Nephtys hombergi* Savigny, 1818 (Annelida: Polychaeta). *Sarsia* 69: 63–68
- Beukema, J. J., De Vlas, J. (1979). Population parameters of the lugworm, *Arenicola marina*, living on tidal flats in the Dutch Wadden Sea. *Neth. J. Sea Res.* 13: 331–353
- Bierzuchudek, P. (1982). The demography of Jack-in-the-pulpit, a forest perennial that changes sex. *Ecol. Monogr.* 52: 335–351
- Boesch, D. F., Wass, M. L., Virnstein, R. W. (1976). The dynamics of estuarine benthic communities. In: Wily, M. (ed.) *Estuarine processes*. Academic Press, New York, p. 177–196
- Brousseau, D. J. (1978). Spawning cycle, fecundity, and recruitment in a population of soft-shell clam, *Mya arenaria*, from Cape Ann, Massachusetts. *Fish. Bull. U.S.* 76: 155–166
- Carey, A. (1962). An ecologic study of two benthic animal populations in Long Island Sound. Ph. D. dissertation. Yale University
- Caswell, H. (1978). A general formula for the sensitivity of population growth rate to changes in life history parameters. *Theor. Populat. Biol.* 14: 215–230
- Caswell, H. (1982). Stable population structure and reproductive value for populations with complex life cycles. *Ecology* 63: 1223–1231
- Charlesworth, B. (1980). *Evolution in age-structured populations*. Cambridge University Press, Cambridge
- Cockburn, A., Braithwaite, R. W., Lee, A. K. (1981). The response of the heath rat, *Pseudomys shortridgei*, to pyric succession: a temporally dynamic life history. *J. Anim. Ecol.* 50: 649–666
- Creaser, E. P., Clifford, D. A. (1982). Life history studies of the sandworm *Nereis virens* Sars, in the Sheepscoot estuary, Maine. *Fish. Bull. U.S.* 80: 735–743
- Davis, W. R. (1979). The burrowing, feeding and respiratory activities of *Nephtys incisa* Malmgren, 1865 (Polychaeta: Annelida). Ph. D. dissertation. University of South Carolina

- Dobbs, F. C., Vozarik, J. (1983). Immediate effects of a storm on coastal infauna. *Mar. Ecol. Prog. Ser.* 11: 273–279
- Doyle, R. W., Hunte, W. (1981). Demography of an estuarine amphipod (*Gammarus lawrencianus*) experimentally selected for high  $r$ : a model of the genetic effects of environmental change. *Can. J. Fish. Aquat. Sci.* 38: 1120–1127
- Gentile, J. H., Gentile, S. M., Hairston, N. G., Sullivan, B. K. (1982). The use of life-tables for evaluating the chronic toxicity of pollutants to *Mysidiopsis bahia*. *Hydrobiologia* 93: 179–187
- Gentile, J. H., Scott, K. J., Lussier, S., Redmond, M. (1985). Application of laboratory population responses for evaluating the effects of dredged material. Technical Report D-85-8, prepared by the US Environment Protection Agency, Narragansett, Rhode Island, for the US Army Engineers Waterways Experimental Station, Vicksburg, Mississippi
- Germano, J. D., Rhoads, D. C. (1984). REMOTS sediment profiling at the Field Verification Program (FVP) disposal site. In: Proceedings of the conference on dredging (1984). Waterway, port, coastal and ocean division, ASCE, Clearwater Beach, Florida, p. 536–544
- Grassle, J. F., Grassle, J. P. (1974). Opportunistic life histories and genetic systems in marine benthic polychaetes. *J. mar. Res.* 32: 253–284
- van Groenendael, J., de Kroon, H., Caswell, H. (1988). Projection matrices in population biology. *Trends Ecol. Evol.* 3: 264–269
- Guillou, M., Hily, C. (1983). Dynamics and biological cycle of a *Mellinna palmata* (Ampharetidae) population during the recolonisation of a dredged area in the vicinity of the harbour of Brest (France). *Mar. Biol.* 73: 43–50
- Heffernan, P., O'Connor, B., Keegan, B. F. (1983). Population dynamics and reproductive cycle of *Pholoë minuta* (Polychaeta: Sigalionidae) in Galway Bay. *Mar. Biol.* 73: 285–291
- Johns, D. M., Gutzjahr-Gobell, R., Shauer, P. (1985). Use of bioenergetics to investigate the impact of dredge material on benthic species: a laboratory study with polychaetes and Black Rock Harbor material. Technical Report D-85-7, prepared by the U.S. Environmental Protection Agency, Narragansett, Rhode Island, for the U.S. Army Engineers Waterways Experimental Station, Vicksburg, Mississippi
- Johnson, R. G. (1973). Conceptual models of benthic communities. In: Schopf, T. J. M. (ed.) *Models in paleobiology*. Freeman Cooper & Co. San Francisco, California
- de Kroon, H., Plaiser, A., van Groenendael, J., Caswell, H. (1986). Elasticity: The relative contribution of demographic parameters to population growth rate. *Ecology* 67: 1427–1431
- Leslie, P. H. (1945). On the use of matrices in certain population mathematics. *Biometrika* 33: 183–212
- Levin, L. A. (1984). Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. *Ecology* 65: 1185–1200
- Levin, L. A., Caswell, H., DePatra, K., Creed, E. L. (1987). Demographic consequences of larval development mode: planktotrophy vs. lecithotrophy in *Streblospio benedicti*. *Ecology* 68: 1877–1886
- Macdonald, P. D. M., Green, P. E. J. (1985). Users guide to program MIX: an interactive program for fitting mixtures of distributions. Ichthus Data Systems, Hamilton, Ontario
- Macdonald, P. D. M., Pitcher, T. J. (1979). Age-groups from size frequency data: a versatile and efficient method of analyzing distribution mixtures. *J. Fish. Res. Bd Can.* 36: 987–1001
- Malinowski, S., Whitlatch, R. B. (1988). A theoretical evaluation of shellfish resource management. *J. Shellfish Res.* 7: 95–100
- McCall, P. L. (1977). Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *J. mar. Res.* 35: 221–266
- McCall, P. L. (1978). Spatial-temporal distributions of Long Island Sound infauna: the role of disturbance in a near-shore marine habitat. In: Wiley, M. L. (ed.) *Estuarine interactions*. Academic Press, New York, p. 191–219
- Morton, R. W. (1983). Status report on disposal operations at the central Long Island Sound disposal site. Contribution No. 25. U.S. Army Corps of Engineers, New England Division, Waltham, Massachusetts
- Olive, P. J. W. (1977). The life history and population structure of the polychaetes *Nephtys caeca* and *N. hombergii* with special reference to the growth rings in the teeth. *J. mar. biol. Ass. U.K.* 57: 133–150
- Olive, P. J. W., Clark, R. B. (1978). The physiology of reproduction. In: Mill, P. J. (ed.) *Physiology of annelids*. Academic Press, London, p. 271–368
- Olive, P. J. W., Morgan, P. J. (1984). A survey of the age structure of beach populations of *Nephtys* spp. in the British Isles. The basis of population fluctuations. In: Boulter, J. (ed.) *Proc. 17th Eur. Mar. Biol. Symp. Oceanologica Acta* (1984) vol. spéc.: 141–145
- Paine, R. T. (1979). Disaster, catastrophe and local persistence of the sea palm *Postelsia palmaeformis*. *Science* 205: 685–686
- Paine, R. T., Levin, S. A. (1981). Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.* 51: 145–178
- Pearson, T. H., Rosenberg, R. (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. mar. Biol. A. Rev.* 16: 229–311
- Peckol, P., Baxter, D. (1986). Population dynamics of the onuphid polychaete *Diopatra cuprea* (Bosc) along a tidal exposure gradient. *Estuar. cstl Shelf Sci.* 22: 371–377
- Pesch, C. E., Zajac, R. N., Whitlatch, R. B., Balboni, M. (1987). The effects of intraspecific density on the life history traits and population growth rate of *Nereis arenacoedentata* (Polychaeta, Nereidae) in the laboratory. *Mar. Biol.* 96: 545–554
- Peto, R., Peto, J. (1972). Asymptotically efficient rank invariant procedures. *J. R. statist. Soc. Ser. A* 135: 185–207
- Pettibone, M. H. (1963). Marine polychaete worms of the New England region. I. Aphroditidae through Trochochaetidae. *Smith. Inst., Bull. U.S. natn. Mus.* 227, Washington D.C.
- Pickett, S. T. A., White, P. S. (1985). The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida
- Pyke, D. A., Thompson, J. N. (1986). Statistical analysis of survival and removal rate experiments. *Ecology* 67: 240–245
- Redman, C. M. (1985). Effect of temperature and salinity on the life history of *Capitella capitata* (Type I). Ph. D. dissertation. City University of New York
- Rhoads, D. C., Aller, R. C., Goldhaber, M. B. (1977). The influence of colonizing benthos on physical properties and chemical diagenesis of the estuarine seafloor. In: Coull, B. C. (ed.) *Ecology of the marine benthos*. Univ. S. Carolina Press, Columbia, P. 113–138
- Rhoads, D. C., Boyer, L. F. (1982). The effects of marine benthos on physical properties of sediments: a successional perspective. In: McCall, P. L., Tevesz, M. J. S. (eds.) *Animal-sediment relations*. Plenum Publishing, New York, p. 3–52

- Rhoads, D. C., McCall, P. L., Yingst, J. Y. (1978). Disturbance and production on the estuarine seafloor. *Am. Scient.* 66: 577–586
- Sanders, H. L. (1956). Oceanography of Long Island Sound X. The biology of marine bottom communities. *Bull. Bing. oceanogr. Coll.* 15: 345–414
- Sanders, H. L. (1960). Benthic studies in Buzzards Bay. III. The structure of the soft-bottom communities. *Limnol. Oceanogr.* 5: 138–153
- Shugart, H., Seagle, T. (1985). Modelling forest landscapes and the role of disturbances in ecosystems and communities. In: Pickett, S. T. A., White, P. S. (eds.) *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, p. 353–368
- Sousa, W. P. (1980). The response of a community to disturbance: the importance of successional age and species' life histories. *Oecologia (Berl.)* 45: 72–81
- Sousa, W. P. (1984). The role of disturbance in natural communities. *A. Rev. Ecol. Syst.* 15: 353–391
- Thompson, J. (1985). Within patch dynamics of life histories, populations and interaction: selection over time in small spaces. In: Pickett, S. T. A., White, P. S. (eds.) *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, p. 253–264
- Tomey, D. (1982). Evaluation and finding of no significant impact for the maintenance dredging of the Black Rock Harbor – Cedar Creek federal navigation channel, Bridgeport, Connecticut. In: *Environmental assessment section 404(b)*. U.S. Army Corps of Engineers, New England Division. p. 8–13
- Valderhaug, V. A. (1985). Population structure and production of *Lumbrineris fragilis* (Polychaeta: Lumbrineridae) in the Oslofjord (Norway) with a note on metal content of jaws. *Mar. Biol.* 86: 203–211
- VanBlaricom, G. R. (1982). Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. *Ecol. Monogr.* 52: 283–305
- Weinberg, J. R. (1985). Factors regulating population dynamics of the marine bivalve *Gemma gemma*: intraspecific competition and salinity. *Mar. Biol.* 75: 173–182
- Weinberg, J. R., Caswell, H., Whitlatch, R. B. (1986). Demographic importance of ecological interactions: how much do statistics tell us? *Mar. Biol.* 93: 305–310
- Whitlatch, R. B., Zajac, R. N. (1985). Biotic interactions among estuarine infaunal opportunistic species. *Mar. Ecol. Prog. Ser.* 21: 299–311
- Whittaker, R. H., Goodman, D. (1979). Classifying species according to their demographic strategy. I. Population fluctuations and environmental heterogeneity. *Am. Nat.* 113: 185–200
- Whittaker, R. H., Levin, S. A. (1977). The role of mosaic phenomenon in natural communities. *Theor. Populat. Biol.* 12: 117–139
- de Wilde, P. A. W. J., Berghuis, E. M. (1979). Spawning and gamete production in *Arenicola marina* in the Netherlands, Wadden Sea. *Neth. J. Sea Res.* 13: 503–511
- Woodin, S. A. (1981). Disturbance and community structure in a shallow water sand flat. *Ecology* 62: 1052–1066
- Yingst, J. Y., Rhoads, D. C. (1978). Seafloor stability in central Long Island Sound. II. Biological interactions and their potential importance for seafloor erodibility. In: Wiley, M. L. (ed.) *Estuarine interactions*. Academic Press, New York. p. 245–260
- Zajac, R. N. (1985). Population dynamics and life history variation in *Polydora ligni* (Polychaeta, Annelida). Ph. D. dissertation, Univ. of Connecticut
- Zajac, R. N., Whitlatch, R. B. (1982a). Responses of estuarine infauna to disturbance. I. Spatial and temporal variation of initial recolonization. *Mar. Ecol. Prog. Ser.* 10: 1–14
- Zajac, R. N., Whitlatch, R. B. (1982b). Responses of estuarine infauna to disturbance. II. Spatial and temporal variation of succession. *Mar. Ecol. Prog. Ser.* 14: 15–27
- Zajac, R. N., Whitlatch, R. B. (1985). A hierarchical approach to modelling soft-bottom successional dynamics. In: Gibbs, P. E. (ed.) *Proc. 19th Eur. Mar. Biol. Symp.* Cambridge Univ. Press, Cambridge, p. 265–276
- Zajac, R. N., Whitlatch, R. B. (1987). The population ecology of *Nephtys incisa* prior to and following dredge spoil disposal in central Long Island Sound. [Hazard Assessment of Dredge Material Disposal: Macro-benthic Post-Spill Population and Community Responses] Final report to the U.S. Environmental Protection Agency, Environ. Res. Lab., Narragansett, Rhode Island
- Zajac, R. N., Whitlatch, R. B. (1988). The population ecology of *Nephtys incisa* in central Long Island Sound prior to and following disturbance. *Estuaries* 11: 117–133

*This article was presented by Professor K. R. Tenore, Solomons, Maryland, USA*

*Manuscript first received: February 1, 1988  
Revised version accepted: June 20, 1989*