

DISTRIBUTION, ADVECTION, AND GROWTH OF LARVAE OF THE SOUTHERN TEMPERATE GADOID, *MACRURONUS NOVAEZELANDIAE* (TELEOSTEI: MERLUCCIIDAE), IN AUSTRALIAN COASTAL WATERS

R. E. THRESHER,¹ B. D. BRUCE,² D. M. FURLANI,³ AND
J. S. GUNN¹

ABSTRACT

Ichthyoplankton surveys in southern Australian coastal waters indicate that larvae of the temperate gadoid, *Macruronus novaezealandiae*, differed consistently in mean size and age between sample sites. These observations are consistent with the hypothesis that larvae are being passively advected by longshore currents from a spawning area on the west coast of Tasmania to habitats along the southeastern and eastern coasts. The ages of larvae at specific points along the advection route vary, which suggests there is considerable variation in rate of larval transport. Rates of larval growth increased exponentially for at least the first 50 days of planktonic life, though the slope of the growth curve varies both between years and between seasons. Growth rates also differ between sampling sites: early stage larvae (<15 d postfirst-feeding) grew more rapidly at sites close to the spawning area, whereas older larvae (>25 d postfirst-feeding) grew more rapidly the farther they were from the spawning area. Migration of *M. novaezealandiae* to a specific spawning area and the subsequent transport of larvae away from this area appears to be an adaptive response by the population to, on the one hand, regional differences in conditions for larval growth and, on the other, changing needs of the larvae at different stages of their development.

Planktonic eggs and larvae of marine fishes are subject to dispersion (= diffusion) and advection (= transport or drift), topics of considerable theoretical and empirical interest to larval fish ecologists (Smith 1973; Wiedemann 1973; Talbot 1977; Okubo 1980; Naganuma 1982; Power 1986). The causes and consequences of diffusion, aggregation and patchiness of larvae are largely unknown due to problems of sampling at an appropriate scale (Hewitt 1981). Advection of larval fishes, however, has been frequently documented and has been studied in some detail (see Norcross and Shaw 1984). Temporal variability in advection can have considerable impact on rates of larval survival (Norcross and Shaw 1984) and has long been suggested to be a major determinant of year-class strength in populations subject to variable current regimes (Walford 1938; Harden Jones 1968; Nelson et al. 1977; Bailey 1981; Parrish et al. 1981). In at least some species, eggs

and larvae are placed in currents that transport them to larval and juvenile nursery areas (Parrish et al. 1981). Even within species, however, the extent of adult migration and larval counter migration varies widely between populations, presumably in response to local hydrographic conditions (Cushing 1986). Eastern North Atlantic gadoid stocks, for example, provide some of the classic examples of adult migration to spawning grounds and subsequent passive drift of larvae to nursery areas (Harden Jones 1968); in contrast, larvae of at least some Western Atlantic stocks of the same species develop entirely in the immediate vicinity of the spawning grounds (O'Boyle et al. 1984, Sherman et al. 1984; Smith and Morse 1985).

By comparison with their Northern Hemisphere relatives, little is known about the reproduction and larval ecology of southern temperate gadoids, despite the fact that several constitute major fisheries. One species, the blue grenadier or hoki, *Macruronus novaezealandiae*, supports such a fishery in Australia and New Zealand, with combined annual landings of approximately 100,000 t (tonnes). Available data indicate that both the New Zealand and Australian populations migrate each winter to discrete spawning areas, located, respectively, on the west coasts of the New Zealand South Island

¹CSIRO Marine Laboratories, GPO Box 1538, Hobart, Tasmania 7001, Australia.

²CSIRO Marine Laboratories, GPO Box 1538, Hobart, Tasmania 7001, Australia; present address: South Australian Department of Fisheries, GPO Box 1625, Adelaide, South Australia 5001, Australia.

³CSIRO Marine Laboratories, GPO Box 1538, Hobart, Tasmania 7001, Australia; present address: Tasmania Department of Sea Fisheries, Crayfish Point, Taroona, Tasmania 7006, Australia.

(Bladodyorov and Nosov 1978⁴; Patchell 1982; Kuo and Tanaka 1984a, b) and Tasmania (Wilson 1981, 1982). These migrations imply a countermigration by either larvae or juveniles back to adult habitats (e.g., Harden Jones 1968; McKeown 1984). Patchell (1982) reported movement of eggs away from spawning areas in New Zealand, and subsequently collected juveniles in coastal habitats hundreds of km from the spawning area. Similarly small juvenile *M. novaezelandiae* have been collected in estuaries and on the coastal shelf along the southeastern and eastern coasts of Tasmania (Wilson 1981, 1982; Last et al. 1983; Bulman and Blaber 1986), over 200 km from the known spawning area.

⁴Bladodyorov, A. I., and E. V. Nosov. 1978. The biological basis of rational exploitation of *Macrurus novaezelandiae*. Unpubl. TINRO manuscr. English translation held by New Zealand Ministry of Agriculture and Fisheries, Fisheries Research Division Library, 7 p.

How juveniles move between the spawning area and these coastal habitats, or even whether this is a rare or common occurrence in the species is unknown. The present study investigated the distribution, sizes, and ages of larval *M. novaezelandiae*, on the basis of which patterns of advection, larval growth, and the relationship between the two could be inferred.

METHODS

Sampling Procedures

Ichthyoplankton samples were collected at approximately two monthly intervals from April 1984 to September 1985. Samples were obtained at fixed stations along nine transects located roughly equidistantly around Tasmania (Fig. 1). Additional samples were obtained in July and August 1985 along

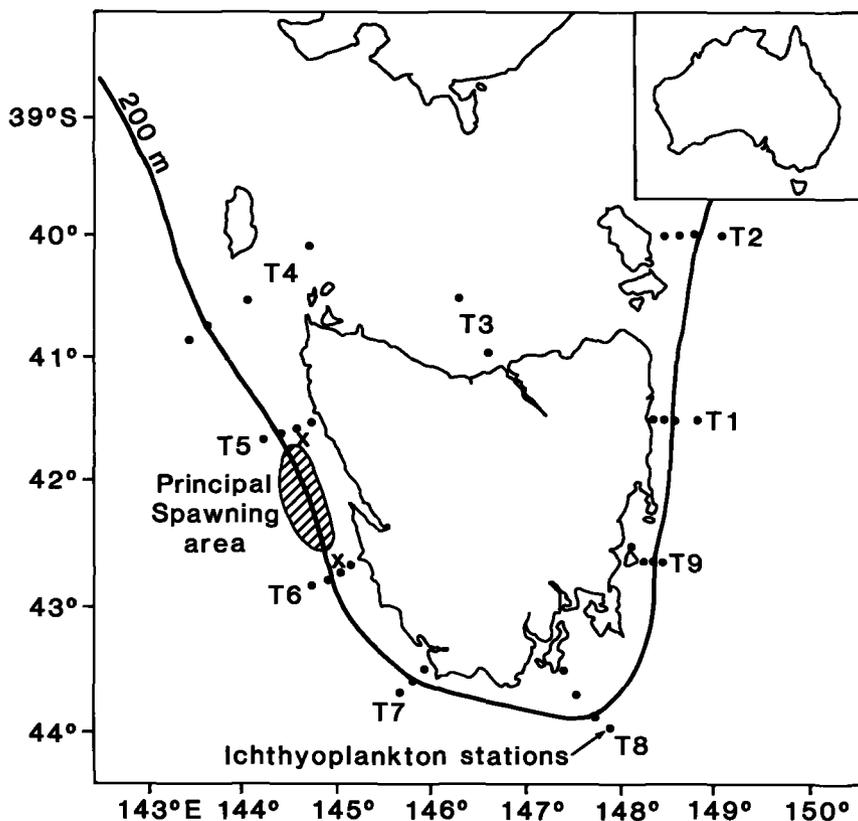


FIGURE 1.—Location of ichthyoplankton sampling sites (solid circles) and release points (X's) of drift cards. The drogued buoy was released at the release point for drift cards south of the spawning area. Cross-hatched area indicates apparent principal spawning area of *Macrurus novaezelandiae* in Australian coastal waters.

the southern coast of mainland Australia (see Figure 3). Transects 1 through 8 consisted of 2–4 stations (4 on average), depending upon the width of the continental shelf. These stations were designated “near-shore” (at a depth of 30–50 m), “midshelf” (70–100 m), “shelf edge” (immediately offshore of the shelf break and usually at a bottom depth of approximately 200 m) and “offshore” (1 nmi offshore of the surface temperature/salinity front between inshore and offshore water masses or, if no front was evident, at 10 nmi offshore from the shelf edge station). In the second year of the study, occasional samples were collected at sites along the west coast between regular transect lines, in order to improve the spatial resolution of analyses and to increase sample sizes.

Two samplers were used: a rectangular midwater trawl (RMT) 1 + 8 (see Baker et al. 1973 for description) and a 1 m diameter ring net fitted with a pivoting bridle system similar to the Tranter-George plankton net (Tranter and George 1972). Mesh sizes for the RMT-8 was 3 mm and 1 mm for the net and cod end, respectively, and 333 μ m throughout for the RMT-1. The ring net consisted of 500 μ m mesh with a 333 μ m cod end. Initially, all sampling was done with the RMT 1 + 8 in a fixed open mode. Because it was difficult to fish the net in rough seas and to calibrate its fishing characteristics (see Pommeranz et al. 1982), the RMT 1 + 8 system was replaced after three cruises (April–August 1984) with the more manageable ring net. The ring net was subsequently used on transects 1 through 8, while the RMT system was retained for study of the vertical distribution of larvae at transect 9.

Each station consisted of a stepped oblique tow made to a maximum depth of 200 m—bottom depth permitting—parallel to bottom contours. The net was fished at 10 m depth steps for three minutes each at a vessel speed of approximately 2 knots. Net depth was monitored continuously by a Simrad⁵ trawl eye. The volume of water filtered was calculated using Rigosha B flowmeters, calibrated in a flume tank. Reported catch rates are standardized to numbers per 1,000 m³ of water filtered. Except where specified below, sampling was not standardized to time of day.

Data on larval depth distributions were obtained with the 1 m ring net off the west coast of Tasmania. Sampling was conducted on 20 and 21 July 1986

between transects 5 and 6, over a bottom depth of 100–120 m. As this site is close to the spawning area of *M. novaezealandiae*, the catches consisted primarily of small larvae. On each tow, the net was sent to depth quickly, allowed to stabilize at the selected depth for 1–2 minutes, and then retrieved slowly on a continuous oblique path. Tows were made in the order of progressively deeper depths. As each tow integrated larval abundance to the maximum depth of the tow, it was assumed that differences in standardized catch rates between adjacent strata reflected larval abundance in the depth range added. Twenty-four tows were made, varying from 15 to 90 minutes and from 10 to 90 m depth. Tows were made in six sets, three during the day (0830–1330) and three at night (2300–0400). Sunrise and sunset were at 0730 and 1700 (Australian Eastern Standard Time), respectively.

Samples were divided by hand into two portions. One portion was fixed in a buffered 3.7% aqueous solution of formaldehyde and the other in 95% ethanol. The former were used to identify larvae; larvae in the ethanol-fixed samples were used for ageing and assessment of growth rates. Larval abundance data are based on both portions for each station. The ages of *M. novaezealandiae* larvae were determined by examination of otolith microstructure, following procedures outlined in Brothers et al. (1976). Whole otoliths were extracted from the larvae and viewed under transmitted light at 720–2500 \times using a Leitz Orthoplan microscope and high resolution, closed-circuit television (Ikigami Model CTC-6000). Otolith features were measured with a sonic digitizer (Science Accessories Corporation Graf/Bar) supported by an Apple 2e microcomputer and a modified version of the Basic program DISBCAL (Frie 1982). Viewed laterally, the otolith measured (the lapillus) was virtually circular; all measurements reported are to the point on the perimeter farthest from the primordium (i.e., the axis of maximum growth). Rates of larval growth are uncorrected for shrinkage. Preliminary results suggest shrinkage (TL) due to alcohol preservation averages approximately 5% and is only weakly correlated with larval size (regression of percent shrinkage against preshrinkage TL, slope = -0.005 , $R^2 = 0.18$, $n = 27$). Shrinkage will affect estimates of absolute growth rates, but the available literature (Theilacker 1980; Fowler and Smith 1983) suggests it should not bias comparisons between growth rates, provided the larvae being compared were collected and fixed in the same manner. Statistical analyses were done using Statview 512+, Vers. 1.1.

⁵Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Validation of Ageing Procedures

Larvae of *M. novaezelandiae* were reared in captivity to determine the age at which otoliths form. Fertile eggs were obtained by stripping running ripe males and females immediately after their capture by trawl on the spawning grounds. Eggs were incubated in 1 L plastic jars, which were filled with seawater, and placed in a seawater bath. Initial incubation temperatures ranged from 14° to 18°C (sea-surface temperature was approximately 14°C). Upon return to the laboratory, eggs were transferred to 2 L glass jars and placed in an aquarium maintained at a constant temperature of 14°C ($\pm 0.2^\circ\text{C}$). Incubation jars were not aerated, and no attempt was made to feed the larvae.

Under light microscopy, otoliths were first apparent in *M. novaezelandiae* embryos 10 hours prior to hatching. At hatching, the sagittae and lapilli were developed and conspicuous. The asterisci were first apparent 3–4 days after hatching. Otoliths from newly hatched larvae characteristically have a conspicuous dark and broad band close to their edge, which is apparently laid down at hatching. Scanning electron microscopy indicated the otolith within this hatching mark consisted of a spherical primordium surrounded by an area with little conspicuous structure. The radius of the hatching mark varied between specimens but did not differ significantly between reared larvae ($\bar{x} = 6.9 \mu\text{m}$, range = 6.7–8.5 μm , $n = 17$) and wild-caught larvae ($\bar{x} = 7.5 \mu\text{m}$, range = 5.3–9.7 μm , $n = 17$) ($P > 0.1$, two tailed t -test).

All wild-caught larvae had a second exceptionally dense and very conspicuous band. The radius of this band varied from 10.2 to 16.4 μm ($\bar{x} = 13.2 \mu\text{m}$, $n = 17$), i.e., approximately 5–7 μm outside the hatching mark. Although the otoliths of reared larvae reached sizes close to this (maximum radius = 13.1 μm), this distinctive band was not evident in their otoliths. As the largest of these larvae had fully ossified jaws and well-developed guts and had all but exhausted their yolk reserves, the second major band in the otoliths may have formed close to or coincident with first feeding. The microstructure of the otolith differed markedly inside and outside of the "first-feeding band". Within its radius, there was little evidence of consistent structuring (other than the hatching mark); beyond the first-feeding mark, increments were unambiguous, increasing in width exponentially. As we saw no indication that any structure prior to the first-feeding mark formed daily, otolith age for the larvae examined is defined as the number of increments external to this

feeding mark. This age is used in analysis of growth and advection patterns, unless otherwise indicated.

Based on the observed incubation time (55–60 hours) and the observed time required for reared larvae held under temperature conditions similar to those during the spawning season to develop to a stage where feeding was possible (6 days) (Bruce 1988), the total age of larval blue grenadier can be estimated as otolithic age + 6 days, with a probable error of about ± 2 days. Hence, date at first-feeding for a particular larva was calculated as date of collection less otolithic age, and date of spawning was date of collection less total age. In general, the development of otolith structure prior to first-feeding of larvae in *M. novaezelandiae* is remarkably similar to that of other gadoids (Radtke and Woodward 1980; Bolz and Lough 1983; Dale 1984), as is the proposed time frame.

The hypothesis that increments in the otolith are formed daily was tested by following cohorts of individuals and determining whether the change in the number of increments matched the known sampling interval (Campana and Neilson 1985; Jones 1986). Larvae were sampled within 0.5 km of a drogue deployed near the spawning grounds (see description of drogue below). Larvae from three plankton tows made near the onset of a 26 h period (0521–0649) were compared with those from two tows made close to its end (0628–0701). The respective samples were pooled because the number of larvae caught in each tow was small. Mean sampling interval between the first and last set of tows was 24.6 hours (1.025 days). Size-frequency distributions of larvae collected are given in Figure 2A. Modal analysis (means and variances unconstrained) for the first sample set indicated the presence of two normally distributed populations, with means at 3.61 and 4.66 mm SL (SE = 0.06 and 0.05, respectively); analysis of the size-frequency distributions of larvae collected approximately a day later also indicates two means, at 4.12 and 4.91 mm SL (SE = 0.29 and 0.07, respectively). The smaller of these two means is poorly defined statistically, however. Re-analysis with the added constraint that larvae grew at the same rate across the size range of the two means (which is a reasonable approximation for such small larvae—see below and Figure 9) indicated means for the first set of samples at 3.62 and 4.65 mm SL, and for the second at 3.86 (which is within one SE of the unconstrained mean) and 4.89 mm SL, which fitted closely observed distributions. The average difference in larval sizes between the first and second set of samples (i.e., mean growth for the 24.6 h period) was 0.24 mm SL. The number of

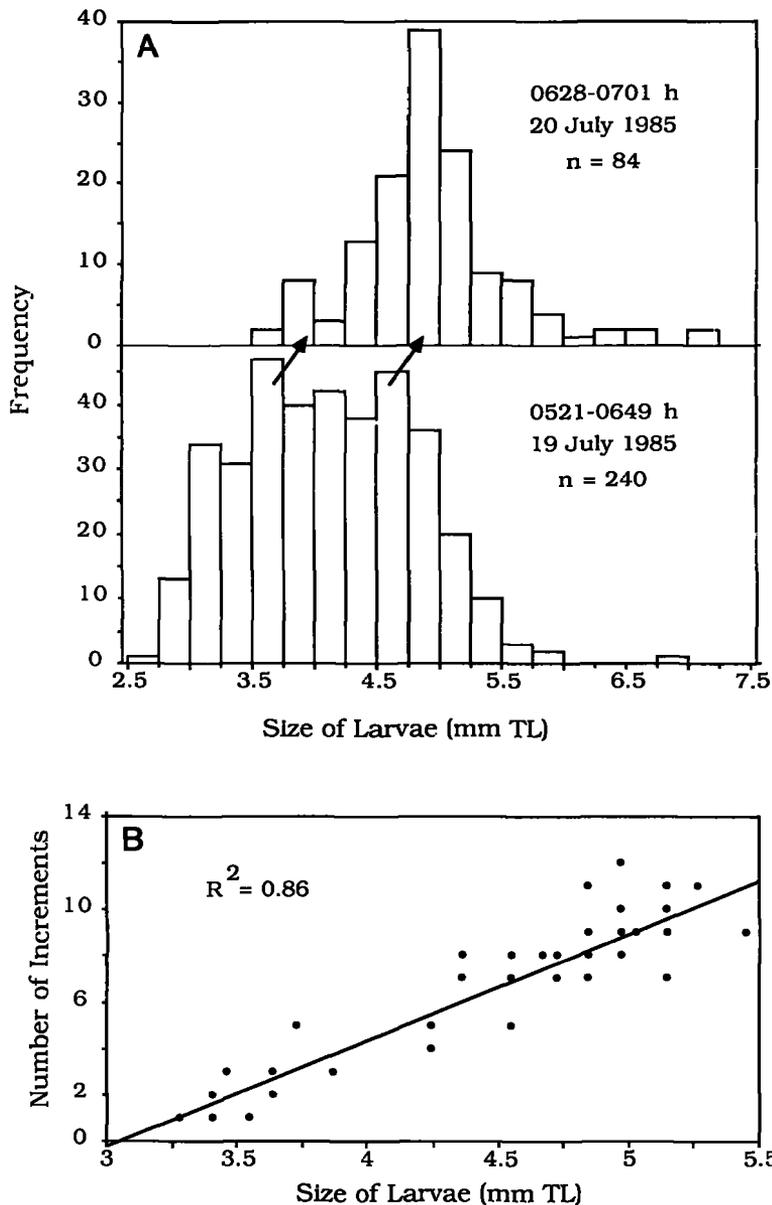


FIGURE 2.—A. Size-frequency distributions of larval *Macruronus novaezelandiae* collected in tows near a drogue at the onset and end of a 26 h sampling period. Arrows indicate apparent progression of the modes. B. Correlation between larval total length and number of postfirst-feeding increments for pooled subsample of larvae drawn from populations in 2A. The correlation is significant at $P \ll 0.01$ and accounts for 86% of the variance in number of increments.

growth increments in these larvae was estimated by drawing subsamples from both populations, proportional to the number of individuals in each 0.25 mm size class, and regressing increment number

against larval size. The relationship is linear and highly significant (Fig. 2B). Based on the least squares regression of increment number on SL, a change in mean larval size of 0.24 mm corresponded

to a change in increment number of 1.102 increments. This compared favorably with the sampling interval, 1.025 days, and is consistent with predictions based on daily increment formation.

Physical Oceanography

Current patterns in the spawning area were investigated in June–August 1985 by 1) release of surface drift cards near the spawning grounds, 2) deployment of a surface drifter drogued at 50 m for 24 hours, and 3) examination of surface isotherms as indicated by a shipboard thermosalinograph.

A total of 2,250 surface drift cards were released during the 1985 spawning season. Cards were released in four lots, two at each of two points (Fig. 1), located immediately north and south of the spawning ground. A set of cards was released at each point on 21 and 22 July and again on 11 and 12 August.

A drifter was deployed at 0800 h on 19 July south of the spawning area at a site at which large numbers of newly hatched larvae were collected (lat. $42^{\circ}43.4'S$, long. $145^{\circ}04.0'E$) (Fig. 1). The drifter consisted a 8.5 m parachute drogue suspended at a depth of 50 m below a large surface buoy fitted

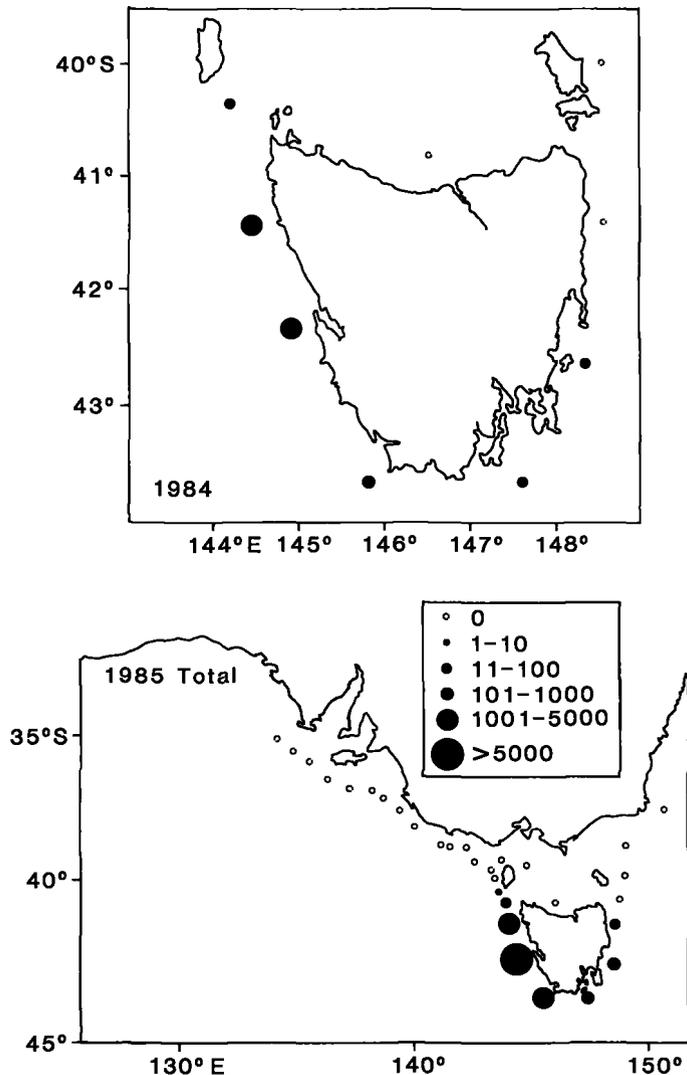


FIGURE 3.—Total catches of larval *Macruronus novaezelandiae*, pooled by transect, for 1984 and 1985, standardized per 1,000 m³ of water filtered.

with a cross-shaped radar reflector and a flashing light. The buoy's position, determined by radar fixes on coastal features, was recorded at 3 h intervals.

Surface temperature and salinity were recorded continuously during all cruises, using a Grundy thermosalinograph. The readings were calibrated against measurements taken during routine hydrographical sampling using depth-profiled CTD and Niskin bottle casts.

RESULTS

Distribution of Larvae

In both 1984 and 1985, *M. novaezelandiae* larvae were caught almost entirely in the winter, peaking

in abundance in July and August, and primarily along the western and southern coasts of Tasmania. The highest densities were caught off the midwest coast (Fig. 3). Larvae were collected in largest numbers at nearshore and midshelf stations (Fig. 4), i.e., at bottom depths of 30–100 m and well inshore of the shelf break, a pattern consistent across all transects.

During depth-stratified sampling, relatively few larvae were caught on tows made at depths <20 m (Fig. 5). Samples taken with the ring net suggest that larvae occurred predominantly between 20 m and 90 m (at a maximum depth of 100–120 m) and that the depth of peak abundance was greater at night (60 m and below) than during the day (approximately 40 m). In a two-factor analysis of variance,

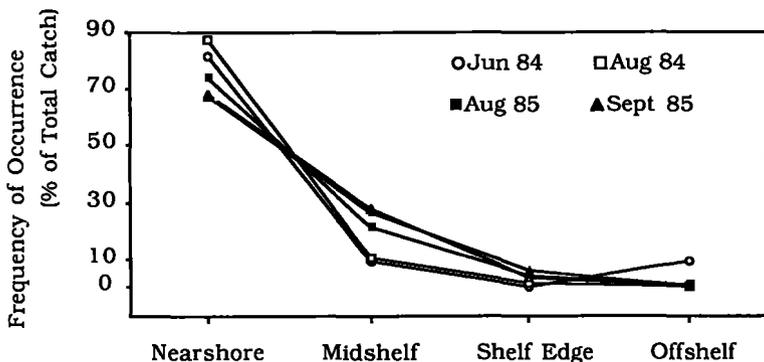


FIGURE 4.—The proportion (percent of total for cruise) of larvae caught on each cruise during the spawning season at each of the four typical sampling positions across the continental shelf.

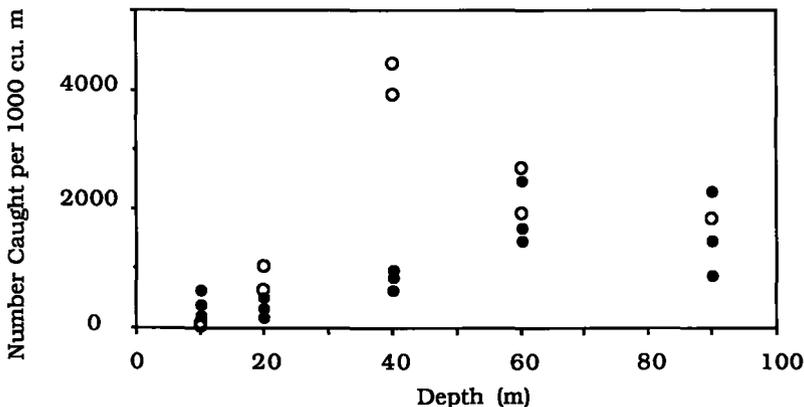


FIGURE 5.—Number of larvae caught during day (open circles) and night (closed circles) periods by oblique tows made to maximum depths ranging from 10 to 90 m. Numbers caught are standardized to 1,000 m³ of water filtered.

depth, time of day, and the interaction term were all highly significant ($F_{3,16} = 22.6$, $F_{1,16} = 13.5$, and $F_{3,16} = 9.6$, respectively, $P < 0.01$ in all cases). Differences between replicate samples were small, accounting for only 12.7% of the variance, despite the same patch of water not being sampled each time.

Although larvae of *M. novaezelandiae* were collected at stations all along the western, southern, and southeastern coasts of Tasmania, the age and size-frequency distributions of these larvae differed conspicuously between collecting sites. In 1984, larvae younger than 5 d postfirst-feeding were caught only on transects 5 (9% of total) and 6 (91%). This is consistent with earlier suggestions (Wilson 1981, 1982) that the area along or on the continental shelf between Sandy Cape (transect 5) and Cape Sorell (transect 6) is the primary spawning area for *M. novaezelandiae* in Australian coastal waters. The

ages of the larvae caught at transect 5 varied widely. From transect 6 south and east along the coast, the ages of larvae collected increased consistently with increasing distance from the spawning area (Fig. 6A). Differences between transects in age distributions of larvae are highly significant ($F_{5,110} = 38.8$, $P < 0.01$), as is the correlation between age and distance (= number of transects, based on the equal spacing of transects along the coast) from transect 5 ($r = 0.64$, $P < 0.01$). The latter correlation was also significant for each of the 1984 spawning season cruises individually, except the last one (September), when all larvae collected were relatively old. Differences between transects in the sizes of larvae caught paralleled differences in ages (differences between transects, $F_{5,110} = 27.9$, $P < 0.01$), with the largest larvae collected farthest along the coast from the spawning area (at transect 9) (cor-

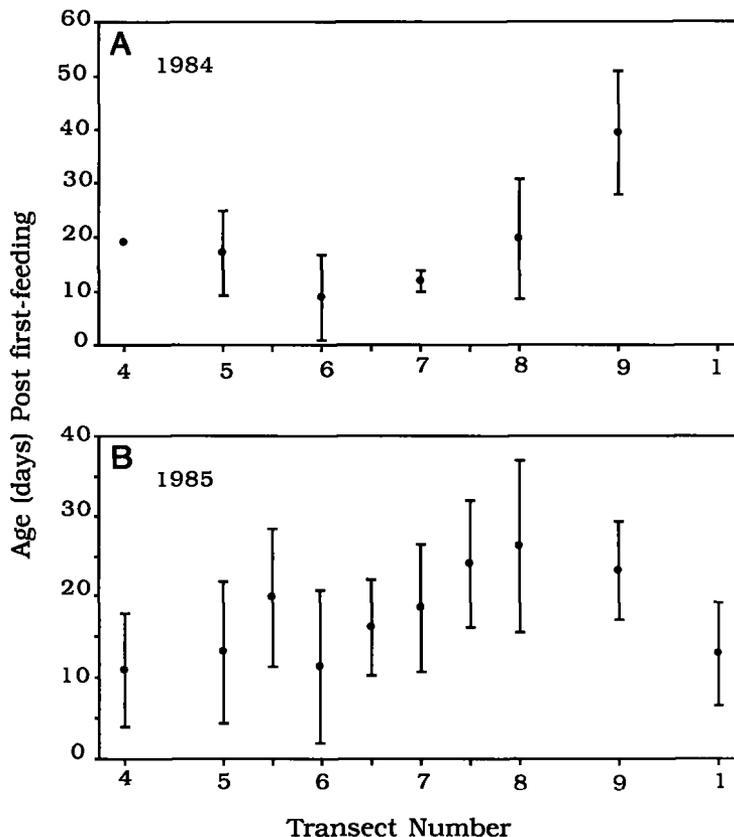


FIGURE 6.—Ages of larvae caught at each transect, pooled across sampling periods, for 1984 and 1985. Vertical bars indicate means ± 1 SD; SE are in all cases < 3 days. Differences in larval ages across transects are highly significant for both years, as are the correlations between age and distance from transect 5.

relation between distance from transect 5 and size, $r = 0.63$, $P < 0.01$).

The relationships between sampling site and larval ages and sizes in 1985 were similar to those in 1984, though apparently complicated by several factors. As in 1984, differences between transects were highly significant ($F_{9,355} = 14.2$, $P < 0.01$, and $F_{9,355} = 12.38$, $P < 0.01$, for age and size, respectively), as were the correlations between both variables and distance from the midwest coast ($r = 0.33$, $P < 0.01$, and $r = 0.36$, $P < 0.01$, for age and size, respectively) (Fig. 6B). At transects 5 and 6, 95% of larvae aged <5 d postfirst-feeding were caught. However, some larvae <5 d postfirst-feeding were also collected at transects 4 and 7, and a few larvae <15 d postfirst-feeding were found off the northeastern coast of Tasmania (near transect 1). The age of the latter is much less than would be expected based on northward advection from the known spawning area (Gunn et al. in press), which suggests strongly the presence of a second spawning area, involving few adults, of the northeastern coast. The occurrence of these larvae confounds a general relationship between distance from the west coast and the ages and sizes of larvae caught. Hence, although for each cruise in 1985 larvae consistently increased in age and size with increasing distance from transects 5 and 6, there was a broad range of larval ages at each transect, relatively old larvae at several transects, and young larvae on the east coast.

Larval Advection

On the basis of the distribution of larvae of different ages and sizes around Tasmania, we hypothesized that most larvae were being carried passively by a longshore current southwards around the coast from the primary spawning area off the west coast. The drift card returns, the movement of the drogue deployed on the west coast, and the distribution of surface isotherms are generally consistent with this hypothesis.

Most drift card returns were from sites southeast along the coast from the release points, including all of those from the first series (July 1985) (Fig. 7A, B). The drogue, deployed at the southern point at the same time drift cards were released, also drifted longshore and to the south (straight-line distance of 11.8 km in 26 hours). Movement of the drogue was conspicuously related to wind speed and direction, varying from nil at slack winds (<9 km/h) (as measured by shipboard anemometer) to slightly >1 km/h for a 9 h period when wind speed averaged

approximately 55 km/h from the northwest (350° magnetic). For the second release series, drift cards returned shortly after being released on 11 August 1985 at the northern site were predominantly from points inshore (east) and slightly north of the release point (Fig. 7C). Of the 43 cards returned from this release, only two were found south of the release point; four, found on mainland Australia, had been transported north more than 150 km. In contrast, southeasterly transport was indicated by the cards released at the southern point on 12 August; only three of 30 returns were from sites north of the release point (Fig. 7D). One of these cards was found on South Arm Beach (southeastern Tasmania) on 27 August 1985. It had drifted slightly over 350 km in 15 days. Additional returns from this release included three cards from New Zealand, one from Flinders Island (northeast of Tasmania), and one from the southeastern coast of mainland Australia. All of these were found several months after being released.

The distribution of surface isotherms also suggests the presence of a southward flowing current along the west coast of Tasmania during the spawning period of *M. novaezealandiae*. In both years of the study, west coast temperature plots in late autumn and early winter were dominated by a tongue of water, 1°–2°C warmer than the surrounding water, that extended southwards along the coast, becoming narrower and cooler to the south (Fig. 8). This tongue of warm water, oriented parallel to the coast, was observed on all winter cruises. Satellite imagery has since documented it to be a regular seasonal feature off the west coast of Tasmania (C. Nilsson, in prep.).

Growth

Otolithic age was determined for 116 larvae in 1984 and 365 larvae in 1985. Growth trajectories (length-at-otolith age) for *M. novaezealandiae* larvae were log linear for both years (Fig. 9), accounting for 96% of the variance in length at age in 1984 and 84% of the variance in 1985. Residuals exhibit no conspicuous systematic deviation from linearity in either year and no marked increase in variance with age. Hence pooled data indicate consistent exponential growth through at least the first 50 days of larval life, with no indication that the rate of growth declined late in larval life. The slope of the semilog regression was steeper, albeit only slightly, in 1984 than in 1985 (0.043 vs. 0.039, respectively, ANCOVA $F_{1,477} = 2.56$, $P < 0.001$), which suggests that growth was more rapid in 1984.

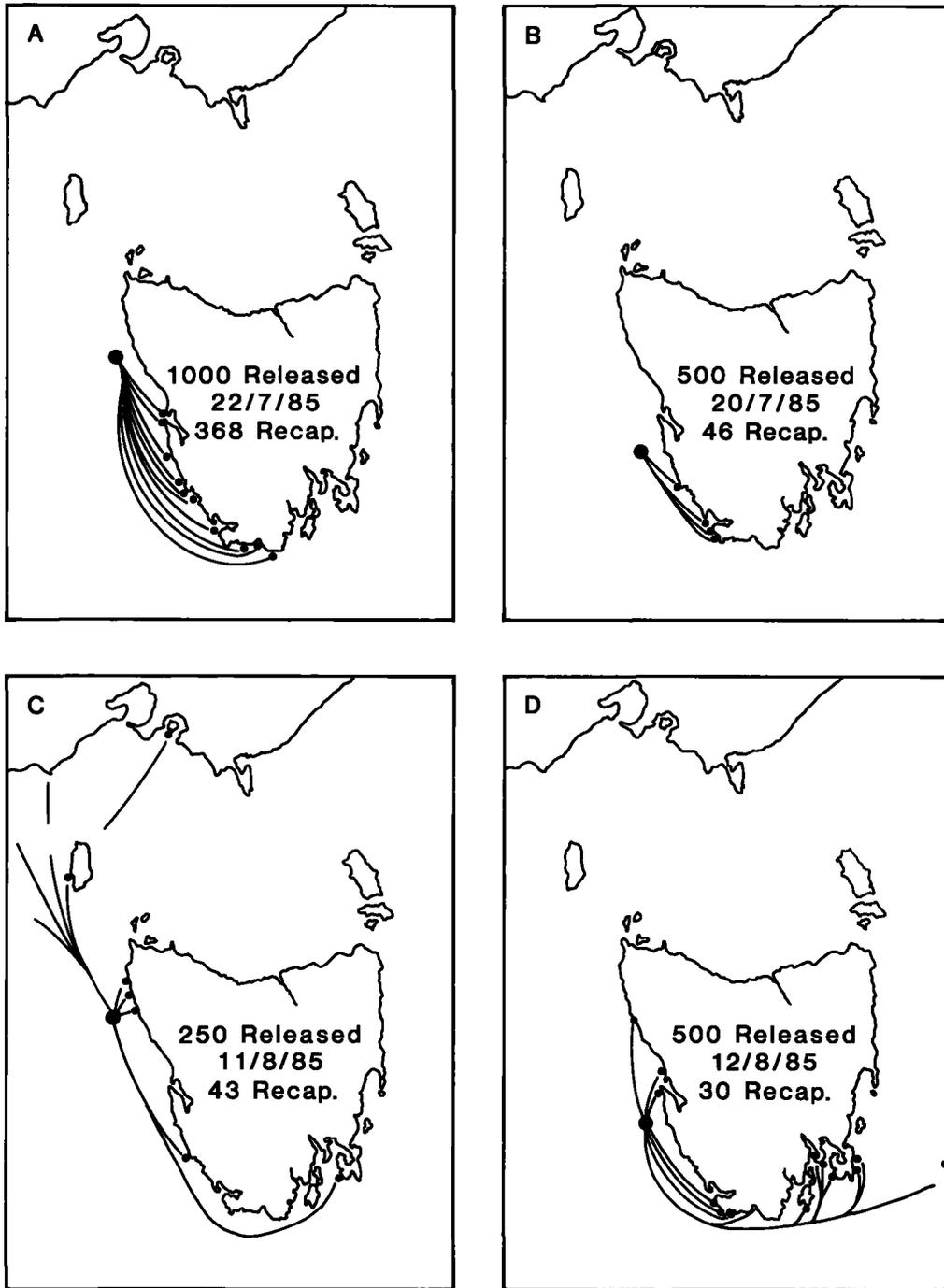


FIGURE 7.—Release and recovery points of surface drift cards for the first (20 and 22 July 1985, A and B) and second (11 and 12 August 1985, C and D).

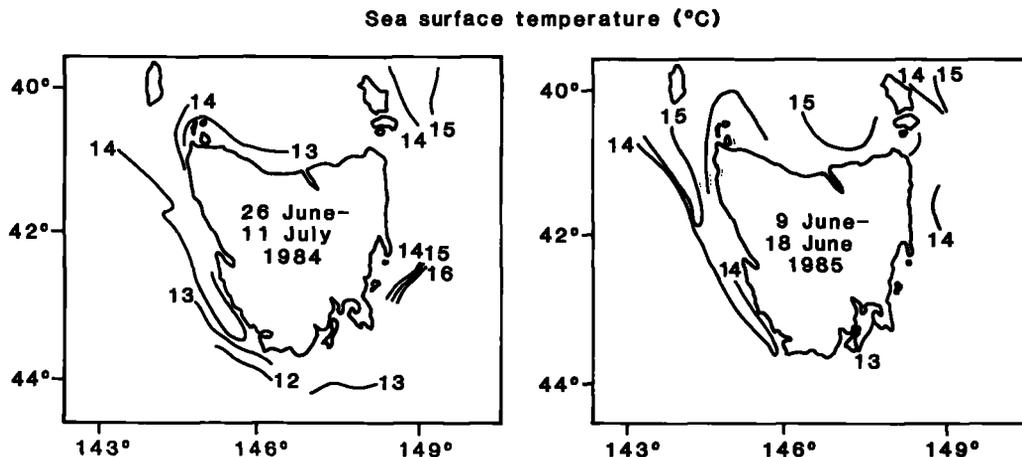


FIGURE 8.—Distribution of surface isotherms during early winter of 1984 and 1985, based on shipboard thermosalinograph traces.

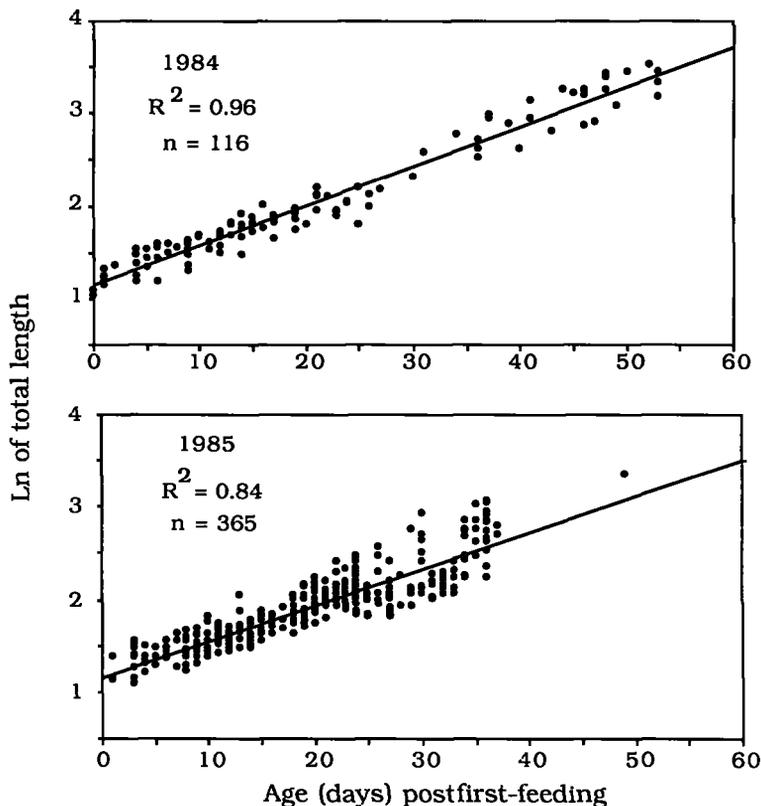


FIGURE 9.—Regressions of ln total length against age (days postfirst feeding) for 116 larvae of *Macruronus novaezelandiae* collected in 1984 and 365 larvae collected in 1985. A semilog regression accounts for 96% of the variance in length at age in 1984 and 84% of the variance in 1985. Differences between years in the slopes of the regressions are significant at $P < 0.01$.

Individual variability in rates of larval growth was assessed by examining the distribution of residuals around the mean exponential growth trajectory for each population each year; a positive residual indicates growth faster than average for the population and a negative one growth slower than average. Analysis of these residuals indicated that rates of larval growth varied seasonally in both years (Fig. 10). Although the variability of rates of larval growth was high within any given period, in both years growth residuals differed significantly for larvae hatched in different months (ANOVA $F_{5,110} = 6.72$, $P < 0.001$, for 1984, and $F_{3,361} = 50.86$, $P < 0.001$, for 1985). In 1984, there was a weak, but consistent tendency for residuals to increase throughout the spawning season (correlation between residual and hatching date, $r = 0.36$, $P < 0.01$). In 1985, deviations from population mean growth rates were

generally negative early in the spawning season, reached a positive maximum during August, and then declined in September.

There was also evidence of a complex relationship between rates of larval growth and location. Overall, the distributions of growth residuals differed significantly across transects ($F_{9,355} = 8.71$, $P < 0.01$), with relative growth rates tending to be highest farthest from the west coast spawning area. The weakness of the correlation between growth rate and distance is due, in part, to two factors. First, there was a marked change in the relationship between location and growth rate with increasing age of the larvae examined. The older the larvae, the more positive the slope between distance from the spawning area and relative growth rate (Fig. 11). For larvae less than approximately 10 d postfirst-feeding, the slope was significantly

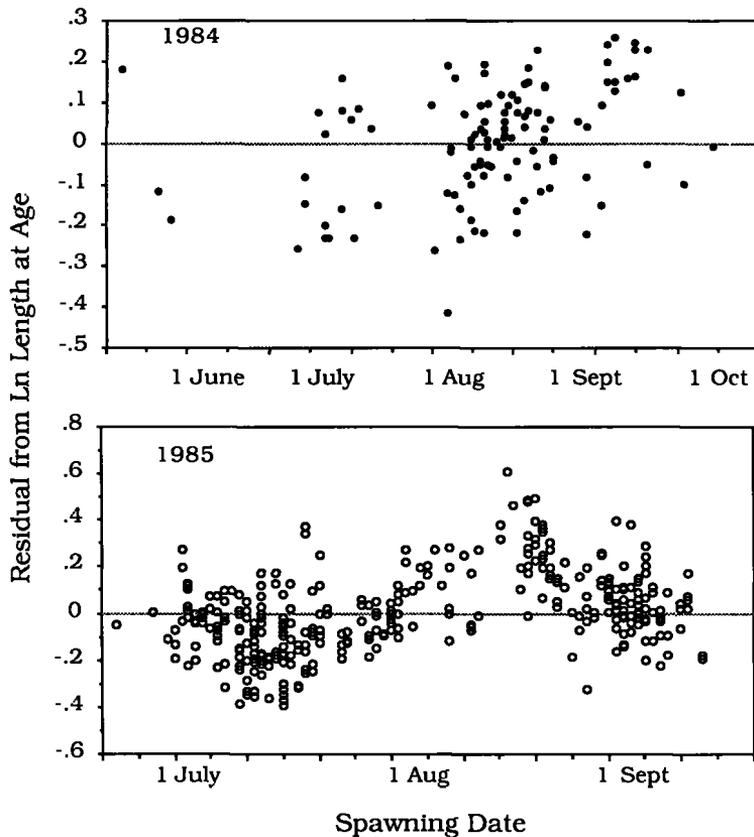


FIGURE 10.—Temporal variation of residuals from the semilog regression of ln total length against age for 1984 and 1985. *Macruronus novaezelandiae* spawning started approximately a month later in 1985 than 1984 (see Gunn et al. in press for details). Differences in residuals for larvae pooled by month of spawning are significant at $P < 0.01$ for both years.

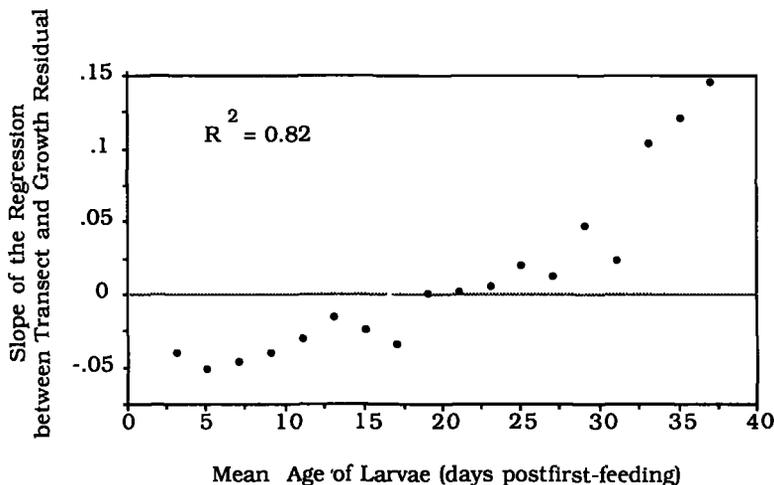


FIGURE 11.—Relationship between age of *Macruronus novaezelandiae* larvae examined (pooled into 3 d increments) and the slope of the regression between relative growth rate (residual from semilog regression of ln total length against age) and transect number. The correlation between slope of the regression line and age class of larvae is significant at $P < 0.01$.

negative; relative growth rates were highest on the west coast, near the spawning area, and declined to the south and east ($F_{1,106} = 20.25$, $P < 0.001$) (Fig. 12). In contrast, for larvae older than approximately 25 d postfirst-feeding, the slope was significantly positive; relative growth rates were lowest on the west coast, increased towards the east coast ($F_{1,124} = 25.58$, $P < 0.001$), and were highest farthest from the spawning area (Fig. 12). The transition from a negative (west coast fastest) to a positive (east coast fastest) slope occurs at a larval age of approximately 17–22 d postfirst-feeding.

The second factor confounding the correlation between distance from the spawning ground and relative growth rates is an apparent seasonal change in the strength of the correlation, particularly for older larvae. A correlation between distance from the west coast and relative growth rates of larvae accounts for 27% of the variance in growth residuals for larvae aged more than 25 d postfirst-feeding in the early, slow-growth portion of the 1985 spawning season. By August, however, during the period when larval growth rates were uniformly high, the correlation accounts for only 10% of the variance in growth rates and, by the end of the spawning season, for larvae hatched after 25 August, the relationship between location and growth rates for these older larvae disappears altogether ($R^2 = 0.02$). There are insufficient data for a comparable analysis of seasonal changes in growth rates of older larvae in 1984.

DISCUSSION

The increase in mean age and size of larvae with increasing distance from the west coast, the pattern of drift card returns, and the distribution of surface isotherms on the west coast of Tasmania during winter all support the hypothesis that larval *M. novaezelandiae* are transported by longshore currents from a spawning ground on the west coast to the southeastern and eastern coasts. This hypothesis is also supported by independent studies of the physical oceanography of the west coast. A southward flowing, longshore current off the west coast in winter was first suggested by Newell (1961); drift bottles he deployed off the coast moved in a similar pattern to our drift cards. Subsequently, Baines et al. (1983) inferred the presence of this current from a shelfward depression of isotherms and confirmed it by the drift pattern of a drogoue released off the northwestern coast. Baines et al. (1983) reported the Zeehan Current, as they named it, to be relatively narrow (approximately 40 km wide) and restricted largely to the edge of the continental shelf. It moves southwards at a depth averaged flow in the order of about 20 km/d (C. Fandry, pers. commun.⁶). This figure is reasonably consistent with our data on larval ages at different points along the advection route. The distance between the spawning ground

⁶C. Fandry, CSIRO Division of Oceanography, GPO Box 1538, Hobart, Tasmania 7001, Australia, pers. commun. June 1987.

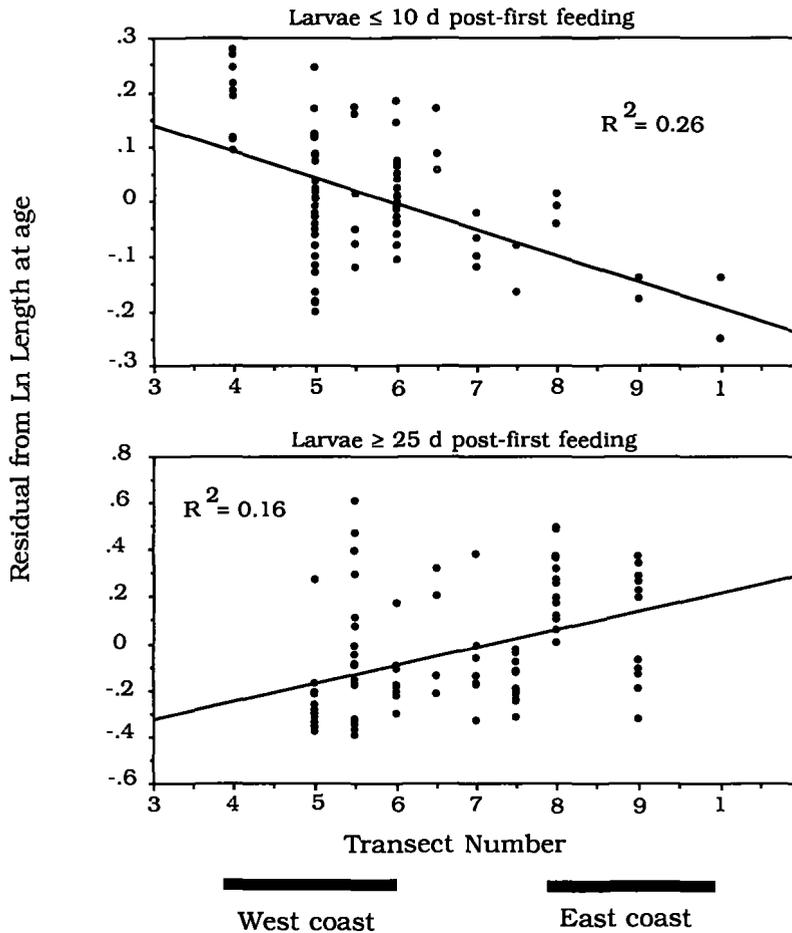


FIGURE 12.—Regressions between relative growth rates and transect number for *Macruronus novaezelandiae* larvae ≤ 10 d postfirst-feeding and those ≥ 25 d postfirst-feeding. Correlations are significant at $P < 0.01$ for both age classes of larvae.

and transect 8, off the southeastern coast, for example, is about 400 km. Hence, the minimum time it should take a larva drifting passively in the mainstream of the current to reach transect 8 would be approximately 20 days. In fact, the shortest interval between release time and recovery of one of our drift cards on the southeastern coast was only 15 days suggesting that at least occasionally larvae could be transported around the southern end of Tasmania very quickly. Total ages of larvae collected at transect 8 varied from 22 to 41 days, averaging 31 days in 1984 and 32 days in 1985. As few larvae are likely to traverse a perfectly direct path between the spawning grounds and transect 8, the mismatch between predicted minimum and observed average ages is probably reasonable and the hypothesis that

larval distributions are the result of passive advection seems plausible.

The range of ages of larvae at each point along the advection route appears to reflect, in part, spawnings by *M. novaezelandiae* at sites north and south of the primary spawning area, in part, the distribution of the larvae relative to the main axis of the Zeehan Current, the location of which is likely to vary with time, and, in part, variations in the strength and direction of that current. Baines et al. (1983) noted that the manifestation of the current may often be overridden by direct wind effects, which is supported by our observations. The drift rate and direction of our drogue varied as an immediate function of wind speed and direction. C. Fandry (fn. 6) suggested that wind affects move-

ment of the water column off the west coast to depths of at least 100 m, i.e., virtually the entire depth range occupied by larval *M. novaezealandiae*. Hence, it is likely that the direction and speed of larval transport vary, though still being predominantly southwards. Such variability is indicated by our drift card data. Drift cards released at the mid-shelf station of transect 5 on 22 July 1985 were recovered inshore and south of the release point; cards released at the same location 19 days later, however, were mostly recovered north of the release point (Fig. 7). Given the depth of the wind-driven effects, it is likely that larval fishes present at that site on the two dates would also have been advected either south or north, depending on temporary conditions of wind and current.

Indeed, some larvae apparently develop wholly off the west coast. In both years of the study, the range in sizes and ages of larvae at transect 5, just north of the spawning grounds, was nearly as wide as those at all other transects combined. On this basis, we suspect that some oceanographic feature on the mid-west coast of Tasmania results in significant retention of larvae in that area. One possibility is that, as larvae are most abundant near shore, some are trapped in relatively static pockets of water near the coast and not entrained in the general southerly current stream. Another possible retention mechanism is a coastal gyre, as yet unreported, that perhaps forms in the winter off the west coast. Indeed, our sea-surface temperature data consistently show a westward bend of surface isotherms immediately offshore of transect 5, which could indicate such a gyre.

Whatever the retention mechanism, a consequence is that larvae vary widely in the location at which they undergo planktonic development. Such variability is not trivial in *M. novaezealandiae*. Apparent rates of larval growth in the species vary significantly both with time and location: faster in 1984 than in 1985, faster in some months than in others, and faster off the west coast for young larvae and off the east coast for older larvae. There are two ways these differences can be interpreted: either the differences are real and reflect variability in conditions that promote growth of larvae, or they are only apparent, deriving not from variations in growth rates, but from growth-dependent mortality that varies in intensity in time and space.

Testing these hypotheses directly in the field is difficult. They can be tested indirectly, however, by examining the distributions of residuals around the population-mean growth trajectories. Consider three possibilities: first, local differences in growth are

real and are determined wholly by food availability; second, local variation is real, but upper and lower limits to growth are determined by physiological constraints inherent in the metabolism of the larvae; and third, real growth rates do not vary locally, but appear to differ due to variably intense selection (predation) against slower growing larvae. The first hypothesis (unconstrained growth) implies normal distributions of growth rates around population means for both fast and slow growing populations; the variance may alter with the mean, but skewness should not. The second hypothesis (constrained growth), however, implies distributions of growth residuals will vary with mean growth rate: the distribution will be negatively skewed (to the left) when mean growth rate is high (more individuals near the maximum growth rate) and positively skewed (to the right) when mean growth rate is low (more individuals near the minimum growth rate). The third hypothesis (growth-dependent mortality) also implies a relationship between the distribution of growth residuals and apparent mean rates of growth, but the relationship is opposite that implied by the constrained growth hypothesis. If predators selectively remove slow growing larvae, such mortality will skew distributions of growth residuals to the right. The greater the intensity of growth-dependent predation (= the higher the apparent mean growth rate), the more positive the skew. Hence, the growth-dependent mortality hypothesis implies that when apparent mean growth rate is low, the distribution of residuals should be normal or only weakly positively skewed; when apparent mean growth rate is high, the distribution should be skewed strongly to the right.

These predictions can be applied to field data for *M. novaezealandiae*. The mean growth rate of larvae was higher in 1984 than in 1985 and, for older larvae, was higher on the south and east coast than on the west coast (too few young larvae were caught on the east coast to warrant a comparison for that age group). The distributions of residuals for 1984 and 1985 are depicted in Figure 13, and those for west and southeast coast populations of larvae older than 25 d postfirst-feeding are depicted in Figure 14. The data are throughout consistent with the constrained-growth-rate hypothesis. As predicted by this hypothesis, the distribution of growth residuals is skewed negatively, albeit weakly, in 1984 ($k_2 = -0.35$, $t = 1.58$, $P < 0.1$), and skewed positively, also weakly, in 1985 ($k_2 = 0.45$, $t = 1.36$, $P < 0.1$). Similarly, growth residuals for the relatively fast-growing larvae caught off the south and east coasts are distributed normally ($k_2 = 0.25$, $t = 0.61$, NS),

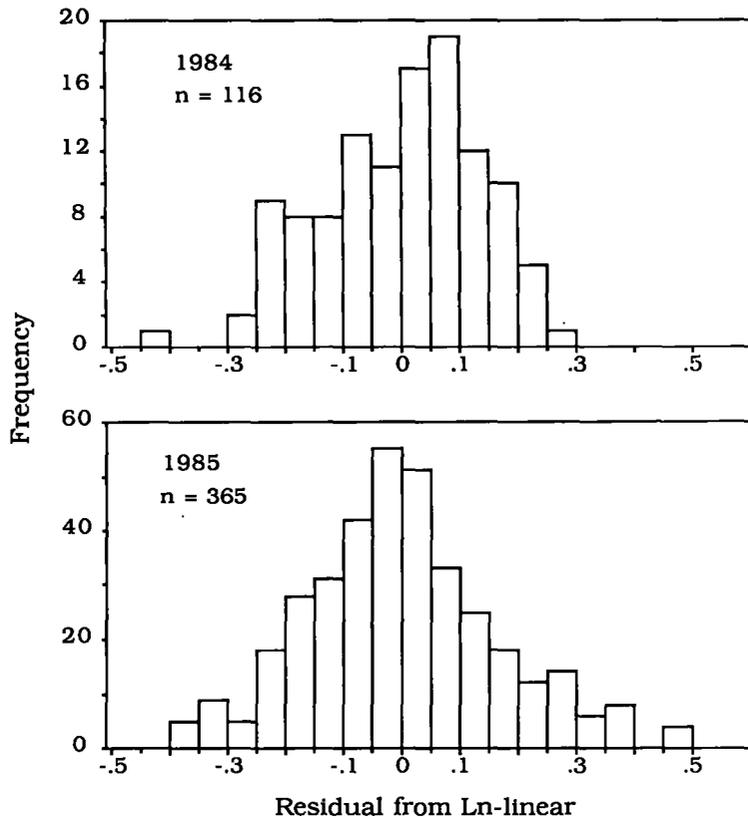


FIGURE 13.—The distribution of residuals about the semilog regression of \ln total length against age of *Macruronus novaezelandiae* for 1984 and 1985, based on growth trajectories pooled by year.

whereas those for the slower growing larvae collected off the west coast exhibit a significant positive skew ($k_2 = 0.68$, $t = 2.76$, $P < 0.01$). We conclude, therefore, that the data are consistent with the constrained growth hypothesis, that variations in rates of larval growth documented in this study are likely to be real, operating within whatever factors constrain the limits of larval growth for the species, and that they reflect variations in environmental conditions that affect growth rates.

Exactly what these environmental conditions are is still not clear, though it is likely they relate to water temperature and food availability. That larvae <15–20 d postfirst-feeding grew faster off the west coast of Tasmania than off the south and east coasts could, for example, reflect the presence of the relatively warm Zeehan Current off the west coast. Growth rates of gadoid larvae increase with water temperature (Lawrence 1978) and temperatures in this current near the spawning grounds

were 1° – 2°C warmer than off the south and southeastern coasts. Circumstantial evidence suggests that regional differences in growth rates of older larvae, in turn, were related to differences in food availability. As noted above, larvae older than 25 d postfirst-feeding grew faster off the east coast than off the west coast early in the spawning seasons. This difference between coasts narrowed later in the season and disappeared altogether late in the spawning season (September). This pattern of spatial and temporal differences in growth was matched by variations in coastal productivity. Harris et al. (1987) reported that in winter (August, referred to by them as “early spring”), autotrophic water column productivity was higher off the east coast in 1985 than off the west coast; reported values for shelf waters ranged from 1.71 to $4.5 \text{ mg C} \cdot \text{m}^{-3} \cdot \text{h}^{-1}$ for the east coast versus 0.06 to 0.84 for the west coast. In September, however, (Harris et al.’s “late spring”), differences in water column

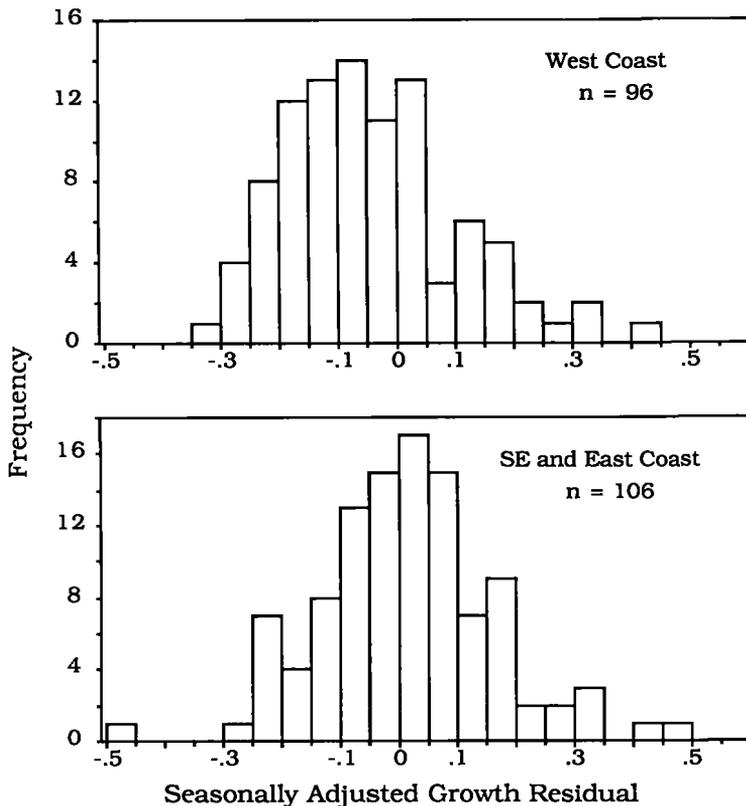


FIGURE 14.—The distribution of seasonally adjusted residuals from the semilog regression of \ln total length against age for *Macruronus novaezelandiae* larvae ≥ 25 d postfirst-feeding for larvae collected off the west coast (transects 5 and 6) and the southeast and east coasts (transects 8 and 9). Residuals were adjusted for seasonal variations in mean rates of larval growth by fitting a polynomial to the seasonal patterns and extracting new, detrended residuals.

productivity between the two coasts were less pronounced; measured values for two sites off the east coast were 1.51 and 2.89 $\text{mg C} \cdot \text{m}^{-3} \cdot \text{h}^{-1}$ versus values for the west coast that ranged from 1.04 to 2.24. We suspect, therefore, that growth rates of these older larvae are driven by local differences in the abundance of copepods and other larger zooplankters that constitute their primary diet. Why such regional differences in productivity did not result in a parallel difference between coasts in growth rates of younger larvae is not known. It may be that the effects of food availability on growth rates of first-feeding larvae are overridden by those of water temperatures.

Regardless of how location affected the growth rates of young and older larvae, summarized in Figure 11, the net effect remains that conditions favorable for early larval growth were not spatial-

ly coincident with those favoring growth by older larvae. Specifically, growth rates of larvae aged <10–15 d postfirst-feeding were highest closest to the spawning area of *M. novaezelandiae*, whereas growth rates of larvae older than 25 d postfirst-feeding increased the farther away from the spawning area the larvae were caught. Why *M. novaezelandiae* aggregate to spawn off the west coast of Tasmania in the winter, rather than at any other site or time, cannot be known. Winter spawnings are not the norm in gadoids (Breder and Rosen 1966; Hislop 1984) nor, with the possible exception of a weak gyre off the coast, is there any conspicuous oceanographic feature or condition, such as a highly localized plankton bloom, yet documented that would uniquely characterize the site as a particularly good one for spawning. Nonetheless, the enhanced growth rates of early stage larvae at the site argue

for a positive selective value for migrating to the west coast to spawn. At the same time, increased rates of growth by older larvae away from the spawning area suggest equally strong selection to ensure that, as they develop, larvae are transported away from the west coast. Larvae achieve the maximum growth rate only by being at the right place at the right stage of their development. Hence, migration of *M. novaezelandiae* to a specific spawning area and subsequent contra-natant migration of larvae away from that spawning area appears to be neither evolutionarily trivial nor solely the result of selection to place eggs and larvae upstream of some specific nursery habitat. Rather, it is an adaptive feature of the reproductive biology of the fish that relates directly to elements of its larval ecology.

Further, if survival of larvae varies with growth rate, as has been widely suggested (Hunter 1981; Rosenberg and Haugen 1982; Folkvord and Hunter 1986), then spatial effects on rates of larval growth can provide a mechanism that links current variability with year-class strength in *M. novaezelandiae*. We have, as yet, no direct evidence for such a link in this species but such a hypothesis has been frequently proposed for marine fishes (Walford 1938; Sette 1943; Harden Jones 1968; Nelson et al. 1977; Parrish et al. 1981). In most cases, however, emphasis has been placed on the adverse effects of advection, in which inappropriate current patterns result in larvae being transported into oceanic habitats not well suited for their development. For example, Devonald (1983) and Theilacker (1986) presented evidence that larval mackerel, *Trachurus symmetricus*, found well off the California coast feed less well and are in worse condition than those collected closer to shore, which is consistent with the adverse effects of offshore transport on year-class strength suggested by Parrish et al. (1981). In contrast, advection is not a negative factor in *M. novaezelandiae*: larvae do better when advected away from the spawning area at the right stage of their development. Such a positive effect of advection is implicit in hypotheses involving spawning grounds, nursery areas, and adult habitats that are spatially separated (Harden Jones 1968; Shelton and Hutchings 1982). Data for most species, however, are still too sparse to determine the general significance of a direct, positive effect of advection on rates of larval growth like that in *M. novaezelandiae*.

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