Abstract.—To enable accurate ageing of orange roughy, *Hoplostethus atlanticus*, eggs caught in egg production surveys for biomass estimation, eggs were cultured at four experimental temperatures, and the results were fitted to a regression model of age-at-stage for the culture temperatures used. Water column ascent and descent rates of early stage eggs were estimated by using a combination of experimental observation and theory. Young eggs ascended rapidly (>300 m·day^{-1}), middle-aged eggs approached neutral buoyancy, and the oldest eggs sank rapidly. The ascent and development rate results were combined with data on water column thermal structure to produce a "thermal history model" of orange roughy egg development, enabling the thermal history of eggs to be considered in ageing them as they rise through the stratified layers into the mixed layer. The ascent and descent rates and modelled depth-at-stage were compared with field data on depth distributions of stages from MOCNESS tows over the North Chatham Rise, New Zealand. For the dominant and subdominant egg stages, predictions closely matched the field results. The model therefore provided a robust method for ageing eggs caught in an egg production survey for orange roughy. The ontogenetic pattern of buoyancy in the eggs may partially explain the distributions of early juvenile orange roughy on the North Chatham Rise. The bias in predicted egg ages, caused by the assumption that temperature of development was constant for eggs below the mixed layer, was shown to be important in egg production estimation.

Manuscript accepted 9 September 1994.
Fishery Bulletin 93:373–385 (1995).

Ascent rates, vertical distribution, and a thermal history model of development of orange roughy, *Hoplostethus atlanticus*, eggs in the water column

John R. Zeldis
Paul. J. Grimes
Jonathan K. V. Ingerson
MAF Fisheries, Greta Point
Box 297, Wellington, New Zealand

Orange roughy, *Hoplostethus atlanticus* (family: Trachichthyidae), are slow-growing, deep water (700–1,500 m) fish that have been found in large quantities mainly in New Zealand[1] and Australia (Kailola et al., 1993). In winter, orange roughy aggregate to spawn near banks, pinnacles, and canyons, and these aggregations attract large amounts of fishing effort. Fisheries for orange roughy began in 1978–79 in New Zealand. The largest fishery is on the Chatham Rise (Fig. 1) where reported catches reached 13,800 metric tons (t) in 1992–93.[1] The stock assessment for the Chatham Rise fishery is based on stock reduction modelling of biomass in which commercial catches, biological parameters, and time series of relative biomass estimates from research trawl surveys are used. The next largest fishery (with reported catches of 9,128 t in 1992–93 [Field et al., 1994]) is off the east coast of New Zealand, and a large proportion of the catch is taken from the winter spawning aggregations on the Ritchie Bank (Fig. 1). The stock reduction analysis for this fishery prior to 1993–94 was based primarily on catch-per-unit-of-effort data which were highly uncertain and made the biomass estimate very uncertain (Field et al., 1994). Consequently, there was a need for a reliable, absolute biomass estimate.

After reviewing aspects of the biology of orange roughy planktonic eggs and adult fecundity, Zeldis (1993) concluded that both the annual egg production method (AEPM; Saville, 1964) and the daily fecundity reduction method (DFRM; Lo et al., 1992) would be feasible for the estimation of absolute spawning biomass of orange roughy on the Ritchie Bank. Both the AEPM and the DFRM were applied during an egg production survey of Ritchie Bank orange roughy biomass in June–July 1993.[2]

Because egg production methods rely on calculating egg production rates from estimates of abundance-at-age of planktonic eggs, a means of ageing the eggs is required. This is done by determining ages of identifiable morphological stages of egg

[1] Annala, J. (Compiler) 1994. Report from the Special Fishery Assessment Plenary, 17 August 1994: stock assessments and yield estimates for ORH 3B, 24 p. Unpubl. rept. held in MAF Fisheries, Greta Point library, Wellington, N.Z.

[2] Zeldis, J., R. I. C. C. Francis, J. K. V. Ingerson, M. Clark, and P. J. Grimes. 1994. A daily fecundity reduction method estimate of Ritchie Bank and east coast North Island orange roughy biomass. Draft New Zealand Fisheries Assessment Research Document. MAF Fisheries, Greta Point, Wellington, N.Z.

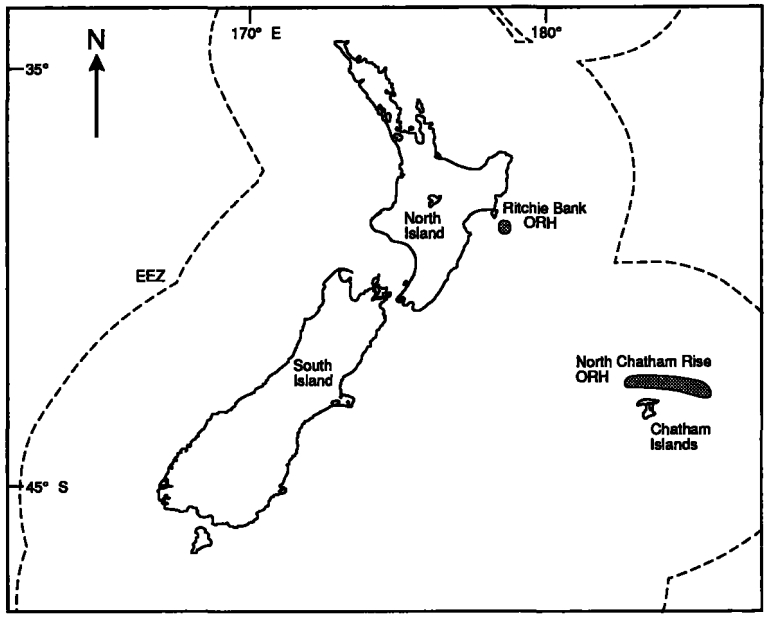

Figure 1

Map of New Zealand and Exclusive Economic Zone and location of Chatham Rise and Ritchie Bank orange roughy, *Hoplostethus atlanticus*, fisheries.

development. Embryogenesis and larval development of orange roughy are undescribed, as are the vertical distributions of the eggs and larvae (Zeldis, 1993). Orange roughy produce large eggs (2.32-mm mean diameter) with a large oil droplet (0.60-mm mean diameter), suggesting that their eggs would be strongly positively buoyant (Robertson, 1981). Since egg development rate in teleosts is strongly temperature dependent (Pauly and Pullin, 1988; Pepin, 1991), changes in the vertical distribution of orange roughy eggs during embryogenesis will have a strong effect on their development rate, because they are spawned in thermally stratified waters below the mixed layer (Zeldis, 1993). Therefore, in order to estimate egg production for orange roughy accurately, a model was needed which considers the thermal history of an egg when the observed stage of development is used to estimate age.

To create and test this model, this study had the following objectives: 1) to describe the temperature dependence of egg development rate; 2) to estimate ascent rates of egg stages with experimentation and theory; 3) to combine results on development rate and ascent rate to develop a 'thermal history model' of orange roughy development in the water column; and 4) to test predictions of this model against observed vertical distributions of egg stages in the water column.

In this study a generalized description of embryology is used to address these objectives. Photographs of some of the egg and larval stages have been published (Grimes and Zeldis, 1993), and detailed descriptions of orange roughy embryological and larval stages will be published separately.

Methods

Embryological, ascent rate and vertical distribution studies were conducted on the North Chatham Rise (Fig. 1) from 7 to 28 July 1992 with the MAF Fisheries RV *Tangaroa*, a 70-m research stern trawler (voyage TAN9206). Additional embryological and ascent rate studies were conducted on the Ritchie Bank from 6 June to 8 July 1993 during an egg production survey (*Tangaroa* voyage TAN9306).

Embryology and development rates

To study embryology and development rates, orange roughy eggs were cultured under controlled-temperature conditions in a shipboard laboratory. The culturing facility had four insulated, plastic 20-L bins, in which plastic jars with mesh tops were submerged to hold the eggs. Each bin had flow-through supplies

of seawater (500 mL·min^{-1}) filtered to 5 microns. Water was cooled to 6°C by a refrigeration system, then heated to desired culture temperatures by aquarium heaters controlled with digital thermistors. The 6°C inlet and heater for each bin were within a central PVC "upwelling stem" driven by an airstone and provided stable culture temperatures during the study (±0.2°C). The jars and bins were disinfected with weak ammonia about every three days.

Culture temperatures used were 6, 8, 10, and 12°C, which spanned the temperature range from the depth of spawning to the sea surface in orange roughy spawning areas. The eggs used for the 6°C culture were fertilized from stripped fish (on voyage TAN9306), and the eggs used for the 8, 10, and 12°C cultures were captured from the plankton (on voyage TAN9206). Growing captured planktonic eggs was generally more successful than starting with stripped eggs and sperm. Only a few hundred strip-fertilized eggs were successfully grown, as opposed to thousands of captured eggs. Strip-fertilizing was most successful when free-flowing, ovulating females and freely expressible males were taken from the wings of the trawl and when cooled seawater and dilute sperm infusions were used with the eggs. The eggs that were selected from the plankton samples for culturing were those that floated in the plankton catches.

Eggs were staged by using the criteria and figures for killifish *Fundulus heteroclitus* from New (1966), in which most relevant features of orange roughy development were identifiable, up to and including New's stage 25. Subsequent stages were defined by the degree the tail was free of the yolk (as a proportion of total tail length), and stage 30 was defined as the hatching stage. Stage numbers used in this paper are assumed to represent the midpoints of the time periods of the stages. Eggs were sampled from the jars and examined under a binocular microscope every 3 or 4 hours at 6°C, and less frequently (see Fig. 2) at 8, 10, and 12°C, until stage 9 (morula formation). The 6°C eggs were sampled more frequently because they were the only culture temperature used on voyage TAN9306 and more time was available to sample and observe eggs. After morula formation, eggs from all temperatures were sampled once or twice a day until stage 19 (blastopore closure) and then once every 1 or 2 days until hatching was imminent. After examination, the sampled eggs were either replaced in the culture vessels (if they were rare) or more commonly preserved in 4% buffered formaldehyde in seawater.

Since the eggs used in the 8°C, 10°C, and 12°C series were caught from the plankton, their absolute ages at the start of their series (at stage 5) were not known. To estimate the absolute ages of the observed stages, the cumulative time up to each stage since stage 5 was regressed against the observed stage for each series for each temperature. This meant all regression lines effectively had a common x-axis intercept at stage 5, with age = 0. The absolute age at stage 5 for each temperature was estimated by continuing the lines to 0 on the x-axis and taking the absolute values of the resulting negative y-axis in-

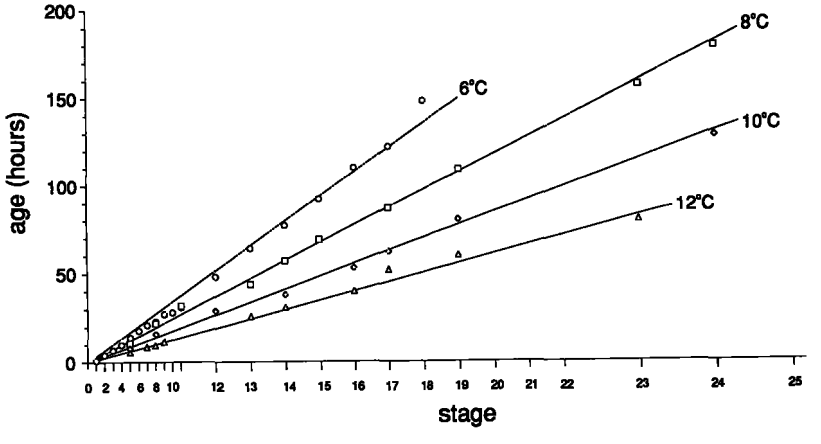

Figure 2

Orange roughy, *Hoplostethus atlanticus*, egg development stages at four temperatures from culturing experiment with curves fitted from Equation 1. The stage numbers should be interpreted as indicating the midpoint of the period of each stage.

tercepts. These predicted y-axis intercepts had small standard deviations (SD) ranging from 1.3 h to 1.5 h, so this source of error in age estimation was considered negligible. The absolute values of the intercepts were then added to the cumulative times of all the observations to estimate the absolute ages for each observed stage for each temperature (Fig. 2). The model was then reestimated by using these absolute ages (the fitted lines in Fig. 2). The regression model predicted egg age as an exponential function of temperature and a linear function of stage:

$$age = 8.803\ e^{-0.158temp} \times stage \qquad (1)$$

The fit had r^2 of 0.96.

The justification for assuming that egg age was a linear function of stage was as follows. The mean duration of the stages given by New (1966) at 20°C for killifish were 1.0 ±0.35 (1 SD) h for stages ≤10, 4.1 ±1.14 h for stages 11 and 21, and 9.0 ±1.15 h for stages 22 and 25. Thus, stage durations were similar within each of these stage groups and differed between the groups by the ratios 1.0: 4.1: 9.0. Evidently, these ratios also applied to orange roughy development, judging by the linear appearance of the orange roughy age-at-stage data for each temperature (Fig. 2) when the x-axis (stage) was scaled by these ratios for stages 1 to 10, 11 to 21, and 22 to 25, respectively. Thus, to use Equation 1 to estimate age from stage, the input value for stage had to be scaled by these ratios (e.g., the appropriate input value for stage 13 would be (11)(1) + (2)(4.1) = 19.2). Orange roughy egg stages from 26 to 30 deviated from that of New (1966) and were not of a consistent length. Therefore, scaling of these stages was not done and ages for stages ≥26 were not modeled.

The justification for assuming that egg age was an exponential function of temperature was that the egg development period for 140 species of pelagic, spherical marine fish eggs was well predicted as an exponential function of temperature and egg size by Pauly and Pullin (1988).

Egg ascent and descent rates

To estimate egg ascent and descent rates, a graduated, perspex cylinder (7×100 cm) was suspended from the ceiling of a shipboard laboratory; its bottom was open in a bucket of seawater and the cylinder was filled with surface seawater (35.00 ppt salinity; see below for the temperatures used). Orange roughy eggs of various stages were introduced at the bottom of the cylinder and, following an initial ascent of 10 cm (to allow the eggs to reach terminal velocity), subsequent ascent was timed over four to seven 10-cm intervals. Older eggs sank; therefore these were introduced to the top of the cylinder and descent rates were measured by following an initial descent of 10 cm. Means and standard deviations of these rates were estimated from estimators for a two-stage sampling design, weighted for unequal subsample sizes (Eq. 5 in Picquelle and Stauffer [1985]).

The water temperature within the cylinder for the experiments on younger eggs (unfertilized, newly fertilized, cell division, and morula-early blastula eggs: stages 0–11 in Fig. 3) was between 6 and 7 degrees and characteristic of the water column at the depth of the spawners. Since these eggs were very positively buoyant, it was clear (see Results section) that the older of these stages occurred shallower in the water column, so it was necessary to predict how fast they would ascend under the temperature-salinity conditions at shallower depths. This was done by using a combination of experimental observation and theory in the following way.

First, it was observed that unfertilized and stage-1 eggs ascended the experimental cylinder at a mean rate of 275 m·day^{-1} at 6°C and 35.00 ppt (Fig. 3). This ascent rate was used to predict the density of these eggs by using the theoretical relationships in Robertson (1981), the seawater density, and seawater viscosity (Sverdrup et al., 1964) in the cylinder. The predicted density was 1.02488 g·cm^{-3}. To test this theoretical density against experimental determinations, the density of unfertilized and stage-1 eggs was measured by diluting the seawater medium (35.00 ppt, 10°C) of the eggs with distilled water until the eggs became neutrally buoyant and by calculating the density of the seawater (1.02425 g·cm^{-3}). The theoretical and experimental densities can be compared if the former value (determined at 6°C) is adjusted to 10°C by using the coefficient of thermal expansion of seawater to account for the decrease in density of the eggs with increase in temperature (taken to be equal in seawater and fish eggs: Coombs et al., 1985). The coefficient of thermal expansion was interpolated from Table 3.1 in Neumann and Pierson (1966) at 35.00 ppt and 8.0°C and atmospheric pressure and was 151·10^{-6} per 1°C change in temperature. The resulting theoretical density was 1.02428, virtually the same density as determined experimentally. This strongly suggests that the theoretically determined density was realistic and that the theory could be used to adapt experimental ascent rates determined at particular temperatures and salinity to various conditions in the oceanic water column.

Accordingly, Robertson's (1981) theoretical relationships were used to calculate the density of stage 1–11 eggs from their experimentally determined

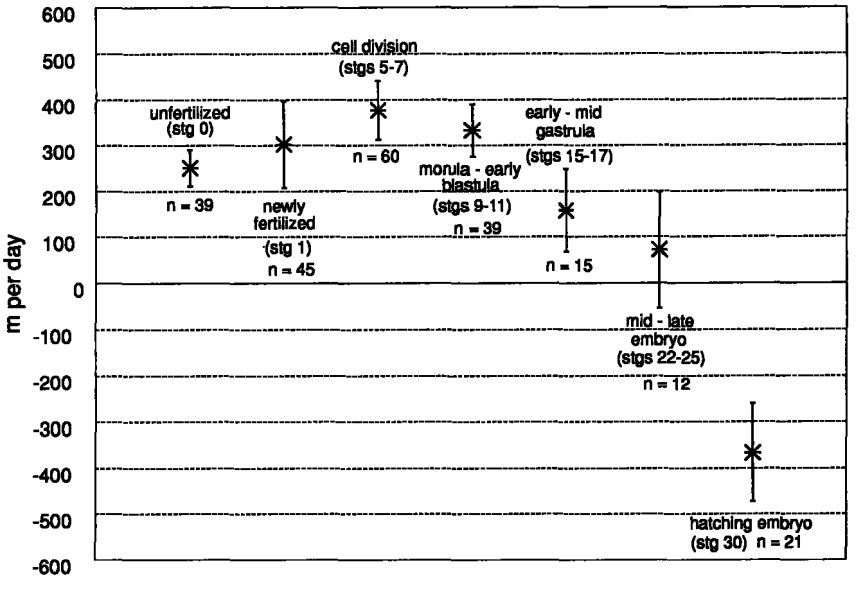

Figure 3

Orange roughy, *Hoplostethus atlanticus*, egg ascent and descent rates in the experimental cylinder for groups of egg stages. Points are means ±95% confidence limits, n = total number of determinations in each group.

ascent rate (mean of 350 m·day^{-1}; Fig. 3) at 6.0°C and 35.00 ppt in the experimental cylinder. This density (1.02406 g·cm^{-3}) and the coefficient of thermal expansion were then used to estimate the ascent rates (Table 1) for stage 1–11 eggs through the water column. This was done for depth strata corresponding to 1°C increases, from 6.0 (the bottom at 870 m) to 11.25°C (the bottom of the mixed layer at 250 m). The analysis accounted for the change in density of the eggs (via the coefficient of thermal expansion), change in density of the surrounding water (from MOCNESS-CTD data), and change in seawater viscosity, as the eggs ascended the water column. Neither the viscosity or coefficient of thermal expansion were corrected to account for changes in salinity and pressure during the ascent (p. 69 in Sverdrup et al., 1964; Table 3.2 in Neumann and Pierson, 1966) because they both changed less than 5% over the salinity and pressure gradients considered here.

Ascent rates of early to mid gastrula and mid to late embryo stages (stages 15–25) were estimated in the cylinder at surface temperature (11–12°C) and

Table 1

Predicted ascent rates of stage 1–11 eggs of orange roughy, *Hoplostethus atlanticus*, at various depths and temperatures in the water column based on relationships between egg density, water column sigma-t and viscosity given by Robertson (1981).

Temp. (°C)	Depth (m)	Salinity (ppt)	Sigma-t (g·cm^{-3})	Viscosity (g sec^{-1}·cm^{-1})	egg density (g·cm^{-3})	Ascent rate (m·day^{-1})
6.0	870	34.40	1.02710	0.0159	1.02406	305.7
7.0	700	34.48	1.02703	0.0156	1.02391	316.9
8.0	550	34.55	1.02694	0.0152	1.02376	330.8
9.0	400	34.65	1.02686	0.0149	1.02361	335.4
10.0	315	34.75	1.02677	0.0146	1.02346	350.8
11.0	265	34.89	1.02671	0.0142	1.02331	360.6
11.25	250	35.00	1.02675	0.0141	1.02327	368.4

salinity (35.0 ppt). These conditions emulated seawater densities that are experienced by eggs at these stages in nature, because the embryos are approaching neutral bouyancy and reside primarily within the mixed layer (see Results section).

The descent rate of hatching-stage eggs (stage 30) was measured at 9.0°C. These eggs were very negatively buoyant and were probably sinking rapidly through the water column. Because surface salinity water was used in the experimental cylinder, the measured descent rate (366 $m \cdot day^{-1}$) is probably an underestimate for waters below the mixed layer because of decreasing salinity. The measured descent rate of these eggs at 9.0°C and surface salinity were used to predict their density: 1.02707 $g \cdot cm^{-3}$. This was then used to predict their descent rates at 9.0°C and 34.65 ppt (the salinity at 9°C in the water column) which was 381 $m \cdot day^{-1}$.

A thermal history model

As orange roughy eggs ascend the oceanic water column, it can be assumed that they will develop at the rate governed by their immediate environmental temperature (Pauly and Pullin, 1988). However, their actual stage at any age is determined by an accumulating average of their previous and present temperatures. A model which enables this "thermal history" of an orange roughy egg to be considered, when the egg's observed stage is used to estimate its age, was created in the following way.

First, it was observed that the temperature-at-depth data for the five MOCNESS profiles (Fig. 4) below the mixed layer had three segments for which the depth change per 1°C change was nearly constant. These were 870 m to 450 m, 450 to 315 m, and 315 to 250 m (the bottom of the mixed layer). These depth changes were divided by the predicted egg ascent rates at each of these 1°C depth intervals (Table 1) to determine the amount of time eggs would spend in each of the 1°C temperature strata. Next, a family of age-at-stage curves was graphed by using Equation 1 from 6.0°C (the near-bottom temperature) to 11.0°C, each curve representing development over an interval of ±0.5°C. Eggs were then "developed" graphically, by moving along the 6.0°C curve until the change in age equalled the amount of time eggs spent in that stratum (in this case 9.4 h, since this stratum was truncated by the bottom at 5.75°C). The point reached was age = 9.4 h, stage = 2.8 (Fig. 5). Then, these stage 2.8 eggs were developed further by "dropping down" to the 7°C curve and moving along it until the change in age was 11.4 h (the length of time required to ascend through the 6.5–7.5°C stratum). The point reached was cumulative age = 20.8 h, stage = 6.7, which was the stage the eggs had reached after accounting for development at 7°C and the previous development at 6°C. This procedure was repeated until eggs were aged through to 11.25°C (at 250 m; the bottom of the mixed layer) at cumulative age = 46.0 h. The eggs at this age were in stage 13. Subsequent egg development to stage 26 occurred in

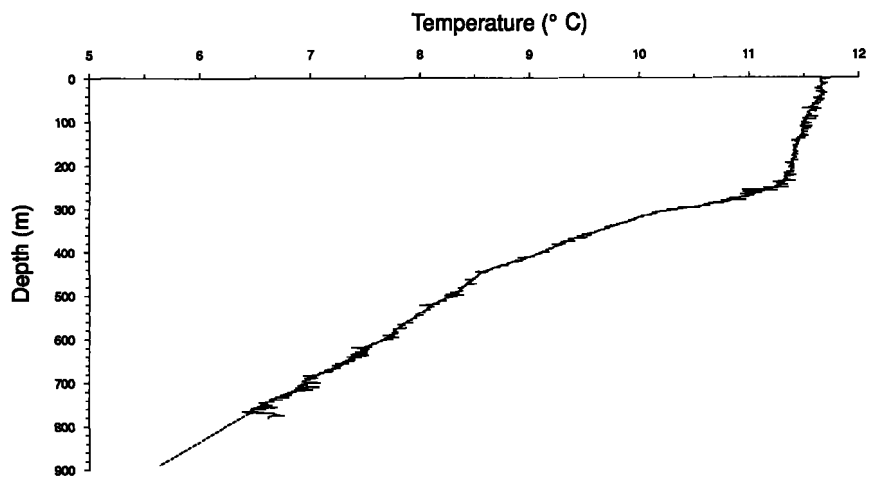

Figure 4

Temperature profile in MOCNESS survey area on the north Chatham Rise during TAN9206. Data are mean temperatures in each 1-m depth stratum across the 5 MOCNESS tows. Temperatures from 780 m to 870 m are extrapolated from temperatures below 450 m for use in modelling.

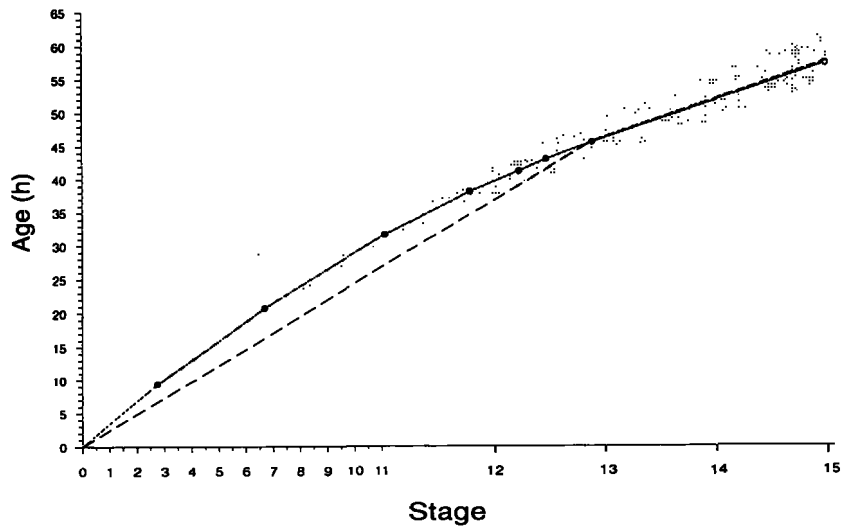

Figure 5

Orange roughy, *Hoplostethus atlanticus*, egg age-at-stage (h) determined from the thermal history model. Dots indicate age-at-stage for each 1°C temperature stratum in the water column. Shaded area shows 95% confidence limits for age-at-stage estimated from 95% confidence limits for ascent rates (Fig. 3). Dashed line shows age-at-stage when temperature of development is assumed to be mean temperature of the stratified layer. Stage numbers represent midpoints of time periods of stages.

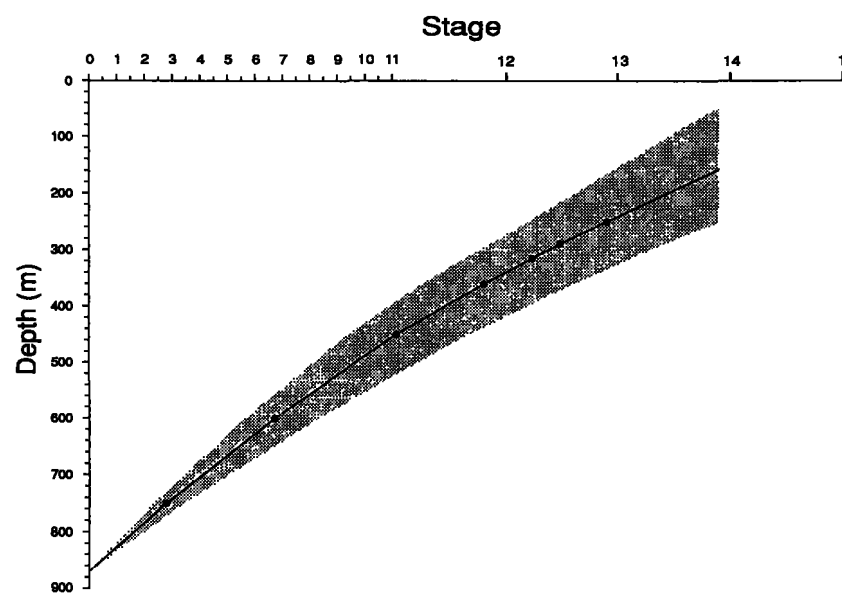

Figure 6

Orange roughy, *Hoplostethus atlanticus*, egg depth-at-stage (m) from surface determined from thermal history model. Dots indicate depth-at-stage for each 1°C temperature stratum in the water column. Shaded area shows 95% confidence limits for depth-at-stage estimated from 95% confidence limits for ascent rates (Fig. 3). Stage numbers represent midpoints of time periods of stages.

the mixed layer, at a constant, mean temperature of 11.25°C, until about cumulative age 150 h was reached (shown only to stage 15 or cumulative age 57.4 h in Fig. 5).

To examine the effect of variability of the laboratory-determined ascent rates on the predictions of age-at-stage, the model was rerun by using the ascent rates in Table 1 ±their 95% confidence intervals (taken to be 60 m·day^{-1} from Fig. 3), to give 95% confidence intervals about the mean age-at-stage. Depth reached at each stage was also determined (Fig. 6) from the ascent rates and time intervals used to run the model, along with the depths reached when the ascent rates ± their 95% confidence intervals were used.

Modeling of age- and depth-at-stage from stage 26 onward was not attempted because of uncertainty in modeling age-at-stage at temperature for these older eggs (see embryology and development rates above). Also, the descent rate data (Fig. 3) were insufficient to describe the rate at which eggs in these stages increase in sinking rate and the position of the eggs in the mixed layer when sinking starts was not known. It is likely that mixing would redistribute neutrally buoyant eggs in the mixed layer before the eggs begin to sink.

Field vertical distribution

To study vertical distribution of eggs in the field, a multiple opening-closing net and environmental sensing system (MOCNESS) was used on the North Chatham Rise to take plankton, temperature, and salinity samples from known depth strata. The MOCNESS tows were made at various times of day in areas where catch rates of adults had been relatively high or where exploratory plankton tows conducted in previous days had produced relatively high catch rates of orange roughy eggs. On three of the MOCNESS tows, the first of the nine nets was used for an integrated haul from the surface to within about 90 m of the bottom at 870 m; then the ascent was stratified into approximately 100-m intervals by the remaining nets (see Fig. 7 for exact stratum intervals). On two of the tows, both descent and ascent were stratified into approximately 200 m intervals. Eggs caught in the tows were either staged on board and then grown in the culture facility or were preserved in 4% buffered formaldehyde in seawater and staged in the land-based laboratory. Preservation had little effect on staging accuracy, because stage frequencies of eggs staged in the laboratory were very similar to those staged in the fresh state on board. However, in three of the nets some of the young eggs had embryos which were damaged and could not be staged with certainty. The damaged eggs were all ≤stage 7 (32 cell); all other samples with eggs older than this had no damaged eggs. The damage was observed prior to preservation and evidently occurred during the hauling of the plankton net. These eggs were staged by proration, from the frequencies of undamaged eggs ≤stage 7 in these nets. In tow 546 (Fig. 7), the nets fishing to 783 and 672 m contained 34% and 32% of eggs damaged, respectively, and the bottom net in tow 545 contained 61% damaged, as percentages of total eggs ≤stage 7.

Field vertical distributions of egg stages (Fig. 7) were compared with their predicted depths from the thermal history model (Fig. 6). To facilitate this comparison, the depth intervals of stages 1 to 14 were determined (Table 2) by using the 95% confidence intervals around the depths reached at the beginning and end of each stage (Fig. 6). These depth intervals were compared with the egg densities-at-stage summed over all MOCNESS tows within 200-m strata (summary column in Fig. 7; Table 3) and with catches from individual nets within these 200-m strata.

Results

Two features were evident in the egg catches from the MOCNESS series. First, the abundance of dif-

Table 2

Predicted mean depth (m) and depth range of egg stages of orange roughy, *Hoplostethus atlanticus*, from the thermal history model. Maximum and minimum depths were predicted from the lower and upper 95% confidence limits in Fig. 6 for the beginning and end of each stage, respectively. The stage numbers represent the midpoint of the period of each stage.

	Depth (m)		
Stage	mean	max	min
1	840	870	800
2	785	840	740
3	740	795	695
4	700	745	645
5	660	710	605
6	625	685	565
7	585	655	530
8	555	625	485
9	520	590	430
10	480	565	415
11	450	535	320
12	335	470	220
13	240	370	100
14	155	285	45

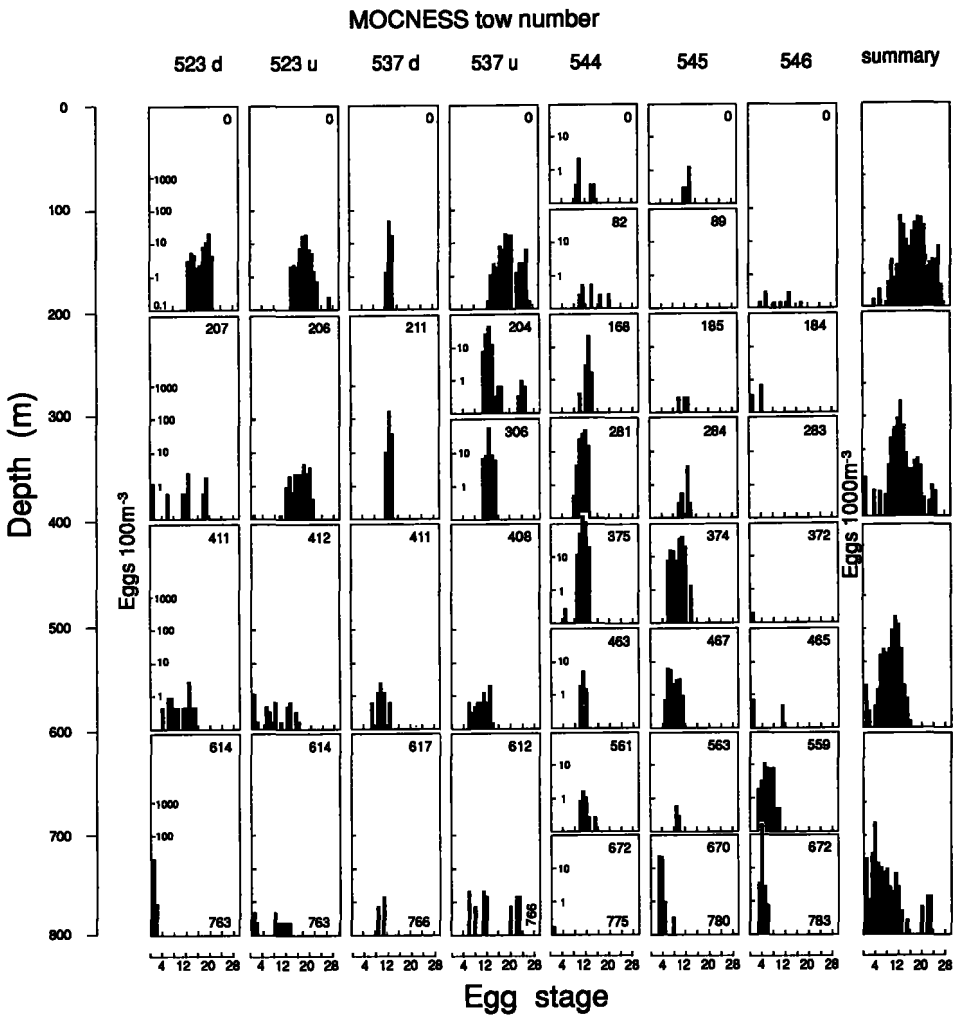

Figure 7

Orange roughy, *Hoplostethus atlanticus*, egg densities-at-stage (standardized to eggs·100 m^{-3}) from the MOCNESS tows conducted over the North Chatham Rise during TAN9206. Tows labelled with 'd' ('u') indicate the descent (ascent) phase of that tow. Box size around each histogram is an approximation of the depth range sampled by that net; the actual minimum depths of each net are annotated (also maximum depths for bottom nets). The "summary" column shows the egg densities-at-stage (standardized to eggs·1,000 m^{-3}) summed over all the tows within each 200-m stratum.

ferent egg stages at the various depths of the MOCNESS nets (Fig. 7) depended on the distance of the tows from concentrations of spawning adults. Two tows were conducted near an aggregation of spawning adults at 177°W (tows 545 and 546; Fig. 8A) in which most eggs were in young and middle ages (up to stage 13) and were caught from the bottom to middle depths (Fig. 7). In three tows conducted to the west of the aggregation (tows 544, 523, and 537; Fig. 8A), most eggs were middle-aged and older and were caught from middle depths to the upper water column. This distribution suggested that the eggs were advecting horizontally away from the spawners as they aged and ascended the water column.

Second, as the eggs developed, their depth changed in a manner consistent with predictions of the ascent and descent rate experiments and the thermal history model (Figs. 3 and 6; summary column in Fig. 7). The young eggs ascended from the spawners toward the surface, middle-aged eggs approached neutral buoyancy in the mixed layer, and oldest eggs sank. In the 0 to 200 m MOCNESS stratum, stage-13

eggs were the youngest to appear in significant quantities (17.9% of total eggs in the stratum; Table 3). The thermal history model (Table 2) predicted that stage-13 eggs should have occurred between 370 and 100 m depth, which is within the sampling ranges of the nets (tow 537, descent) which caught the great majority of them (Fig. 7). Stage-14 eggs were predicted to be from 285 to 45 m (Table 2), and these eggs were found evenly distributed between the 1–200 and 200–400 m strata (Table 3). Stage-15 to stage-26 eggs approached neutral buoyancy (Fig. 3) and accumulated in the mixed layer on the basis of their high proportional occurrence (Table 3; summary column in Fig. 7).

Table 3

Percentages of orange roughy, *Hoplostethus atlanticus*, eggs occurring in each stage for each 200-m stratum sampled by the MOCNESS (derived from the summary column in Fig. 7). Given stratum depth ranges are only approximate: see Fig. 7 for actual sampling depth ranges of the nets.

	MOCNESS stratum			
Stage	0–200 m	200–400 m	400–600 m	600–800 m
1	0.0	0.2	0.3	5.6
2	0.0	0.0	0.0	0.3
3	0.0	0.0	0.0	8.0
4	0.0	0.1	0.0	68.4
5	0.0	0.0	0.2	4.1
6	0.1	0.1	2.7	3.0
7	0.0	0.0	4.0	2.1
8	0.0	0.0	3.1	2.7
9	0.1	0.6	4.1	0.7
10	0.8	4.2	16.0	0.5
11	0.2	8.7	40.3	1.9
12	0.5	16.1	23.8	0.7
13	17.9	53.6	4.3	0.1
14	9.8	10.3	0.3	0.0
15	3.3	1.5	0.1	0.0
16	2.0	0.5	0.0	0.0
17	6.1	0.5	0.0	0.0
18	11.2	0.8	0.0	0.0
19	16.9	1.0	0.0	0.0
20	15.8	0.6	0.0	0.2
21	9.2	0.0	0.0	0.0
22	0.5	0.0	0.0	0.4
23	0.6	0.0	0.0	0.4
24	0.8	0.1	0.0	0.0
25	0.8	0.1	0.0	0.0
26	2.1	0.0	0.0	0.0
27	0.1	0.0	0.0	0.0

In the 200 to 400 m MOCNESS stratum, stages 12 and 13 were most common (Table 3), and the model (Table 2) predicted that these stages would be centered in this stratum. Stages 11 and 14 were also common (Table 3). Their expected mean depths were 50 m deeper and shallower than this stratum, respectively (Table 2), and most of the stage-11 and stage-14 eggs in this stratum were caught in the deeper and shallower parts of it (tows 544 and 537, ascent, respectively; Fig. 7). Eggs approaching neutral buoyancy were caught in the upper part of this stratum (tow 537, ascent), which could be expected since this net sampled the lower mixed layer.

In the 400 to 600 m MOCNESS stratum, the dominant stages were 10, 11, and 12 (Table 3). The model (Table 2) predicted that all these stages would be most common in the upper half of this stratum, and the nets that caught the great majority of them were in tows 544 and 545, fishing between 467 and 374 m; Fig. 7). Of the total eggs in this stratum, 4.3% were in stage 13, which was unexpected from the model, even taking into account the modelled ranges of occurrence (Table 2). It is likely that a low rate of misidentification of stages (between stages 12 and 13) caused these unexpected results. This would be expected of any staging system that attempts to place eggs into discrete categories when they are actually undergoing a continuous growth process.

In the 600 to 800 m MOCNESS stratum, the dominant stage was 4 (Table 3). This stage was predicted to occur between 745 and 645 m (Table 2) which was within the sampling range of the nets that caught the great majority of them (tows 545 and 546, fishing between 783 and 670 m; Fig. 7). The next most abundant stage was 3 and was predicted to occur between 795 and 695 m. The deep net on tow 545 caught most of these eggs and fished between 780 and 670 m. Tow 537 (ascent) caught some older eggs (stages 20–24) that evidently were sinking. These eggs were somewhat younger than were predicted to sink (Fig. 3), suggesting that there is some variability in the stage when sinking begins.

In summary, over all depth strata the predictions of modelled depth-at-stage were consistent with depth distributions of the dominant and subdominant stages caught in the MOCNESS tows. This consistency suggests that the basic parameters of the model are sound and are reasonably well estimated. One factor that might have caused the expected vertical distributions of eggs to deviate from the observed distributions may have been significant amounts of spawning far off the bottom. However, there was no evidence of this, in that significant numbers of very young eggs were seen only in the deepest stratum (Fig. 7, Table 3), and no "spawning plumes" of fish

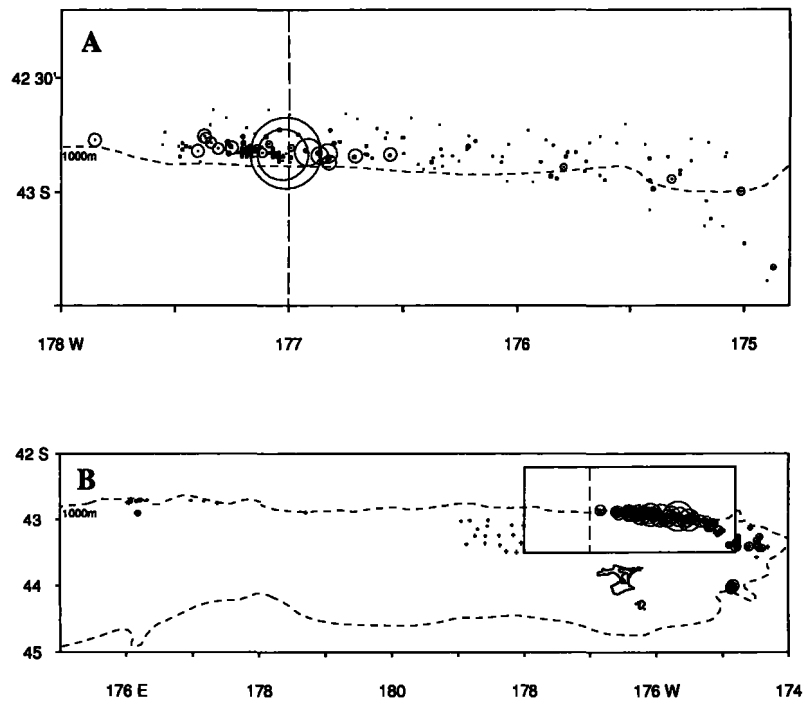

Figure 8

(**A**) Start positions (crosses) of MOCNESS tows on North Chatham Rise for orange roughy, *Hoplostethus atlanticus*, eggs, and start positions and relative adult catch rates (circle areas) from trawls conducted coincidentally with this study on TAN9206. MOCNESS tow numbers from west to east are 544, 523, 537, 546, and 545. (**B**) Relative catch rates (circle areas) of 0+ and 1+ (≤6 cm tail length) juvenile orange roughy during juvenile surveys done in 1988 and 1989 (Mace et al., 1990). Crosses show that tow positions and crosses with no circle had zero catch rate. The inset is the area of the survey shown in (A) and the dashed vertical line indicates the longitude of the spawning aggregation in (A).

(Pankhurst, 1988) were seen on echo sounders during these surveys.

Discussion

In culturing experiments, orange roughy eggs hatched after 235 h of development at 10°C. This was close to the prediction of Pauly and Pullin (1988) that the development period for orange roughy eggs at egg diameter 2.32 mm and 10°C would be 217 h. This result is in the upper part of the scatter in Pauly and Pullin's plot of development period vs. temperature (their Fig. 1), which would be expected, because orange roughy eggs are relatively large and will take longer to develop than will smaller eggs when both are measured at the same temperature (Pepin, 1991).

The eggs changed from positive to neutral to negative buoyancy as they aged (Fig. 3). This was unlikely to have been caused by poor condition of the cultured eggs, because many eggs were neutrally buoyant when captured and were later grown to hatching. Also, older eggs, all of which had been sitting on the bottom of the culture vessels for some days during late development, had virtually 100% hatching success. Finally, late-stage eggs were caught in MOCNESS samples deep in the water column (Fig. 7), albeit in low numbers. This ontogenetic pattern of change in bouyancy is a common one in marine fish eggs (reviewed by Page et al., 1989) and could be the consequence of density changes in the egg as high initial concentrations of yolk are converted to embryonic tissue during ontogeny (Mangor-Jensen and Huse, 1991).

Thus, it is likely that orange roughy eggs undergo extensive movement (both in ascent and descent) through the water column as they develop. Young eggs ascend rapidly to the mixed layer, reaching it

by about age 50 h (stage 13), where they reside until about age 150 h (stage 26); then they sink rapidly for about 50 more h before hatching. Since the hatching eggs sink at about 381 m·day^{-1} and their density is greater than seawater near the bottom in the spawning area on the North Chatham Rise (870 m), they may hatch near the bottom. This vertical distribution pattern of the eggs may partially explain the distributions of early juvenile orange roughy on the North Chatham Rise. The spawning aggregation at 177°W (Fig. 8A) forms each year and has supported the highest measured orange roughy biomasses on the North Chatham Rise since the inception of the trawl surveys on the stock (Zeldis, 1993). There are high concentrations of 0+ to 1+ annual cohort orange roughy about 50 to 175 km east of this aggregation (Fig. 8B; Mace et al., 1990) and this is the only area on the rise where early juveniles have been found in large quantities. Mean, residual currents are directed eastwards along the North Chatham Rise (Heath, 1983; Chiswell, 1994). These currents are generally weak (about 6 cm·sec^{-1} in the mixed layer), and the current velocity decreases with depth (Heath, 1983; Chiswell, 1994). During their 10-day development period, orange roughy eggs spend about 6 days in the mixed layer and a total of about 4 days ascending to and sinking out of the mixed layer. Therefore, on average, eggs spawned in the aggregation at 177°W would be expected to drift somewhat less than 50 km east before hatching near the bottom. The subsequent distribution of the newly hatched larvae is unknown, but since the larvae are more dense than bottom waters of the North Chatham Rise (Grimes and Zeldis, unpubl. data) they may remain near the bottom and drift into the area of high 0+ and 1+ juvenile density just downstream.

In this study, middle-age and older eggs were displaced in near-surface waters some 18 km to the west of the concentration of spawning adults (Figs. 7 and 8A), contrary to the expected eastward drift. This unexpected location may have resulted from smaller-scale eddy and tidal flow embedded in the large-scale mean eastward flow on the North Chatham Rise (Chiswell, 1994).

This study has determined the age-at-stage of orange roughy egg development as vertical distribution changes during ontogeny. These results were formerly unknown for this species. They are, however, essential for egg production estimation of orange roughy biomass where they are used for estimating egg mortality rates and rates of egg production at spawning. A further step is to ask how sensitive egg production estimation is to inaccuracies in egg age determination. This is significant in regard to other studies which may have less information than this one on vertical distributions of eggs during ontogeny. An example is the egg production study by Lo et al. (1992) for Dover sole, *Microstomus pacificus*, biomass, in which eggs were aged on the assumption that the temperature of development was the mean temperature of the stratified layer for the eggs they found in that layer. This assumption does not use depth-specific development rates to age eggs in the stratified layer and if it were applied to orange roughy, would cause egg age to be underestimated (dashed line in Fig. 5). To examine this effect on orange roughy egg production estimates, these underestimated egg ages were used to estimate the production rate of orange roughy eggs from the Ritchie Bank egg production survey and were compared with the result when the thermal history model (solid line in Fig. 5) was used to age eggs. Maximum likelihood fits of both sets of egg abundance-at-age data were done by using only stages ≤10, because older eggs were advected out of the survey area.[2] Egg production rate was biased upward by 31% for the fit with underestimated ages relative to the fit in which ages from the thermal history model were used. This happened because the same numbers of eggs-at-age were assumed to have occurred but over a shorter time for the fit with underestimated ages.

Dover sole eggs have a similar diameter and spawning depth range to that of orange roughy eggs (Lo et al., 1993). Therefore, they should ascend the water column at a similar rate, excluding large differences in water column density and egg density. Therefore, the ages of young Dover sole eggs may be underestimated by a similar extent as shown above for orange roughy, and their production rate may be similarly overestimated when they are aged without using depth-specific development rates. Thus, it seems prudent to reduce ageing bias by using a method that accounts accurately for thermal history of eggs. This is especially important if eggs found below the mixed layer contribute exclusively or substantially to the data set used for estimating egg production. This was the case for the Ritchie Bank egg production survey and has been suggested by Lo et al. (1993) for future Dover sole egg production surveys.

The consistency between the thermal history model results and field results on orange roughy egg vertical distributions suggests that age-at-stage should be predictable in other orange roughy spawning areas (e.g. the Ritchie Bank) where egg production surveys are conducted, provided data are available on water column density and temperature structure. It should also be possible to age other pelagic fish eggs by using depth-specific development rates, as long as ascent rates are not affected by chorionic sculpturing (Robertson, 1981). This would require data

on egg size, egg density, temperature dependent development rates, and water column density and temperature structure.

This study appears to be the first to model the depth-specific development rate of teleost eggs. Orange roughy eggs also appear to have the deepest distribution of any eggs for which a development rate has been studied in detail (see literature summary in Page et al., 1989); most studies have concerned continental shelf dwelling stocks. These two points are probably related, in that it is probably not important to model depth-specific development rate for eggs that are spawned in shallow water where the water column is either completely mixed or has a relatively small vertical thermal gradient (e.g. Coombs et al., 1985; Page et al., 1989). However, if a shelf-dwelling stock spawns near the bottom in stratified waters (e.g. in summer) and if the eggs are small and rise slowly, the development rate of the younger stages of these eggs might be variable with depth to an extent sufficient to significantly affect egg production estimates.

Acknowledgments

The authors thank the officers and crew of RV *Tangaroa* and J. P. Ots for technical assistance, and I. J. Doonan and R. I. C. C. Francis for statistical assistance.

Literature cited

Chiswell, S. M.
1994. Acoustic Doppler Current Profiler measurements over the Chatham Rise. N.Z. J. Mar. Freshwater Res. 28: 167–178.

Coombs, S. H., C. A. Fosh, and M. A. Keen.
1985. The buoyancy and vertical distribution of eggs of sprat (*Sprattus sprattus* and Pilchard (*Sardina pilchardus*). J. Mar. Biol. Assoc. (U.K.) 65:461–474.

Field, K. D., R. I. C. C. Francis, J. R. Zeldis, and J. H. Annala.
1994. Assessment of the Cape Runaway to Banks Peninsula (ORH 2A, 2B, and 3A) orange roughy fishery for the 1993–94 fishing year. New Zealand Fisheries Assessment Research Document. MAF Fisheries, Greta Point, Wellington, N.Z., 24 p.

Grimes, P. J., and J. R. Zeldis.
1993. Early life of orange roughy revealed. New Zealand Professional Fisherman 7(1):84–85.

Heath, R. A.
1983. Observations on Chatham Rise currents. N.Z. J. Mar. Freshwater Res. 17:321–330.

Kailola, P. J., M. J. Williams, P. C. Stewart, R. E. Reichelt, A. McNee, and C. Grieve.
1993. Australian fisheries resources. Bureau of Resource Sciences, Department of Primary Industries and Energy and the Fisheries Research and Development Corporation, Canberra, 422 p.

Lo, N. C. -H., J. R. Hunter, H. G. Moser, P. E. Smith, and R. D. Methot.
1992. The daily fecundity reduction method: a new procedure for estimating adult fish biomass. ICES J. Mar. Sci. 49:209–215.

Lo, N. C. -H., J. R. Hunter, H. G. Moser, and P. E. Smith.
1993. A daily fecundity reduction method of biomass estimation with application to Dover sole *Microstomus pacificus*. Bull. Mar. Sci. 53(2):842–863.

Mace, P. M., J. M. Fenaughty, R. P. Coburn, and I. J. Doonan.
1990. Growth and productivity of orange roughy (*Hoplostethus atlanticus*) on the north Chatham Rise. N.Z. J. Mar. Freshwater Res. 24:105–119.

Mangor-Jensen, A., amd I. Huse.
1991. On the changes in buoyancy of halibut, *Hippoglossus hippoglossus* (L.), larvae caused by hatching-a theoretical view. J. Fish Biol. 39:133–135.

Neumann, G., and W. J. Jr. Pierson.
1966. Principles of physical oceanography. Prentice-Hall, Englewood Cliffs, 545 p.

New, D. A. T.
1966. The culture of vertebrate embryos. Acad. Press, London, 245 p.

Page, F. H., K. T. Frank, and K. R. Thompson.
1989. Stage dependent vertical distribution of haddock (*Melanogrammus aeglefinus*) eggs in a stratified water column: observations and a model. Can. J. Fish. Aquat. Sci. 46:55–67.

Pankhurst, N. W.
1988. Spawning dynamics of orange roughy, *Hoplostethus atlanticus*, in mid slope waters of New Zealand. Environ. Biol. Fishes 21(2):101–116.

Pauly, D., and R. V. Pullin.
1988. Hatching time in spherical, pelagic, marine fish eggs in response to temperature and egg size. Environ. Biol. Fishes 22(4):261–271.

Pepin, P.
1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Can. J. Mar. Aquat. Sci. 48:503–518.

Picquelle, S., and G. Stauffer.
1985. Parameter estimation for an egg production method of northern anchovy biomass assessment. *In* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, p. 7–15. U.S. Dep. Commerce, NOAA Technical Report NMFS 36.

Robertson, D. A.
1981. Possible functions of surface structure and size in some planktonic eggs of marine fishes. N.Z. J. Mar. Freshwater Res. 15:147–153.

Saville, A.
1964. Estimation of the abundance of a fish stock from egg and larval surveys. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 155:164–173.

Sverdrup, H. U., M. W. Johnson, and R. H. Fleming.
1964. The oceans: their physics, chemistry, and general biology. Prentice-Hall, Englewood Cliffs, 1087 p.

Zeldis, J.
1993. The applicability of egg surveys for spawning stock biomass estimation of snapper, orange roughy and hoki in New Zealand. Bull. Mar. Sci. (53)2:864–890.