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Spatial Variability of Recent Otolith Growth and RNA Indices in Pelagic Juvenile *Diaphus kapalae* (Myctophidae): an Effect of Flow Disturbance near an Island?

Iain M. Suthers

School of Biological Science, University of New South Wales, Sydney, NSW 2052, Australia.

Abstract. In February 1993, the pelagic juvenile myctophid *Diaphus kapalae* was sampled with a neuston net in the southern Coral Sea in a region of flow disturbance north of Cato Reef, and to the east in the free stream (northerly flow at 30 cm s^{-1}). There was no significant difference in the size (11–16 mm SL) or age (45–74 days after hatching) between the two regions. Recent growth indices derived from the width of the peripheral daily growth increments (~10 μm each) revealed enhanced otolith growth 38 km downstream and up to 4 days before capture. No significant difference was found for times longer than a week before capture, consistent with fluctuation of the wake indicated from current-meter data. Daily increment formation was confirmed by marginal increment analysis. Recent otolith growth was correlated with the RNA content adjusted by dry weight, which also revealed significantly higher condition in the wake region. Recent growth was correlated with microzooplankton biomass, recorded with an optical plankton counter.

Introduction

The condition, or health, of larval and juvenile fish is a means of assessing the significance of oceanographic features for fish populations during the critical planktonic stage of early life history. Flow disturbance occurs downstream of oceanic islands, generated by each island acting as a stirring rod within the predominant circulation (e.g. Barkley 1972; Emery 1972; Heywood *et al.* 1990; Boehlert *et al.* 1992; Boehlert and Mundy 1993). Nutrient-laden deep water may be drawn into the euphotic zone, stimulating in one example a fivefold increase in the biomass of chlorophyll (Simpson *et al.* 1982). Horizontal characteristics of this flow disturbance may include increased phosphate concentrations downstream (Mackey *et al.* 1987), enhanced chlorophyll concentrations (Simpson *et al.* 1982) and an altered distribution of zooplankton (Hamner and Hauri 1981). Alternatively, little or no effect may be observed (Dandonneau and Charpy 1985; Le Borgne *et al.* 1985; Rogers 1994), possibly owing to the variety of oceanographic conditions and spatial/temporal scales (Le Borgne *et al.* 1985; Cowen and Castro 1994).

Vertically, upwelling is characterized by an upward doming of the thermocline (by over 60 m in Heywood *et al.* 1990). The thermocline is associated with the nutricline and increased chlorophyll concentration (Furnas and Mitchell 1986) as well as increased abundance of larval fish (Loeb 1979).

Upwelling due to flow disturbance can extend over an area some 20 times the island area (Simpson *et al.* 1982). This effect, along with other sources of new nutrient (runoff, and endo-geothermal upwelling, Rougerie *et al.* 1992), may be crucial to the fishing and tourist industries of many islands in the South Pacific, as this is the only source of new production around many isolated islands situated in depths >1000 m. Other sources of new nutrient such as continental shelf waves, tidal inflows and geostrophic suction occur at scales of 100–1000 km (Griffin and Middleton 1986; Nof and Middleton 1989), which cannot generate upwelling around small steep-sided atolls. Studies of adult fish foraging (Rogers 1994) and of fishing activity in island wakes (Johannes 1981) have indicated the importance of flow disturbance, but no study has examined the trophic significance of island wakes for larval fish.

Do the elevated concentrations of chlorophyll observed in island wakes ultimately contribute to the condition of larval fish? Many indices have been used to determine nutritional condition in larval fish, involving morphological (e.g. Ehrlich *et al.* 1976), histological (e.g. Ehrlich *et al.* 1976; Theilacker 1986; Martin and Wright 1987) and biochemical techniques (e.g. Buckley 1984; review in Ferron and Leggett 1994). The RNA–DNA condition index adjusts the amount of protein synthesis, as indicated by the amount of RNA, by the size of the larva, as indicated from the number of cells and the amount of DNA. In the form of a ratio, this index can discriminate starved larvae from fed larvae within 3–4 days (Martin and Wright 1987; Westerman and Holt 1994) and has been used to discriminate between gadid larvae from stratified and mixed conditions on Georges Bank (Buckley and Lough 1987).

Recent daily growth increments of the otolith are another method of assessing larval growth and condition in relation to prey availability in the ocean (e.g. Govoni *et al.* 1985;

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Bailey 1989; Suthers *et al.* 1989). Although otolith growth is considered to respond conservatively to starvation (Molony and Choat 1990; Milicich and Choat 1992), the width of recent growth increments in larvae can respond within days of dietary change (Govoni *et al.* 1985; Eckmann and Rey 1987; Bailey and Stehr 1988; Maillet and Checkley 1990; Suthers and Sundby 1993). Furthermore, recent growth increments and RNA–DNA measures were found to be correlated in larval plaice (Hovenkamp 1990; Hovenkamp and Witte 1991).

The aim of this study was to compare the condition indices, derived from RNA and recent otolith growth, of pelagic juvenile myctophids between an area of flow disturbance in the lee of an island and the free stream. The condition indices were intercompared and correlated with zooplankton biomass, determined with an optical plankton counter.

Materials and Methods

Study Area

Cato Reef is an isolated reef in the southern Coral Sea (23·2°S,155·5°E), approximately 350 km off the coast of Rockhampton, Queensland. Rising from a depth of 2000 m to the surface over a horizontal distance of 50 km or less, the reef itself is approximately 10 × 15 km at the 100-m isobath and breaks the surface in two places (Fig. 1). The nearest reef is Wreck Reef, approximately 130 km north-north-east. During 16–21 February 1993 a northward flow of approximately 30 cm s^{-1} was observed with an acoustic Doppler current profiler (ADCP); it resulted in a region of flow disturbance that extended to at least 300 m depth (limit of ADCP). This region extended 70 km north of the island (Fig. 1). The wake was also manifest by an upward doming of the isotherms by 40–60 m. Currents were probably influenced by the passing of Tropical Cyclone 'Oliver', which was located for two days about 300 km north-north-west of Cato, with winds up to 80 kn. Full physical and biological descriptions of the island wake are in preparation.

Two transects of three stations each were established: one perpendicular to the flow (eastern transect, Stations E1, E2 and E3) and the other through the wake region (northern transect, Stations N1, N2 and N3) (Table 1, Fig. 1). Water temperatures averaged 25.7°C (range 25.6–25.8°C) between 5 m and 25 m depth during the investigation. Each transect was sampled in a night, with replication of the middle station before dawn. Sampling was replicated over three nights for each transect (Table 1).

Pelagic juvenile myctophids were captured in replicated neuston tows at each station with a square-mouthed plankton net (mouth area 75 cm^2, mesh size 300 μm). A flowmeter was situated in the mouth of the net, and all tows were at 1–2 m s^{-1} for 5–8 min. Myctophids were jet-black in colour (range 11–16 mm standard length, SL, see Tables 2 and 3) and were easily separated from the zooplankton. They were stored either in liquid nitrogen within 10–30 min of net retrieval (for RNA–DNA analysis) or in vials of 95% alcohol (otolith analysis). Larvae were not present or not sufficiently abundant for all 18 night × station combinations, and replicate nights were therefore pooled by station for condition analyses (see Tables 2 and 3).

During each tow, an optical plankton counter (OPC, Sprules *et al.* 1992) was deployed over the stern, which provided zooplankton biomass abundance in the size range between 300 and 2500 μm equivalent spherical diameter (esd), roughly equivalent to that retained by 300 μm mesh. Data were restricted to the 5–25-m depth range, for comparison with the neuston net tows.

Table 1. Description of stations and transects

Date in February 1993, latitude (°S), longitude (°E), bathymetry at station (m), distance from 100-m isobath (km) and mean temperature (°C) from 5 to 25 m

February	Station	Latitude	Longitude	Bathymetry	Distance	Temp.
16, 19, 21	E1	23·25	155·68	1057	6·2	25·7
	E2	23·23	155·77	1422	14·6	25·8
	E3	23·22	155·91	1810	29·3	25·8
17, 18, 20	N1	23·15	155·55	294	3·4	25·6
	N2	23·03	155·53	1441	15·8	25·6
	N3	22·89	155·52	1744	37·7	25·8

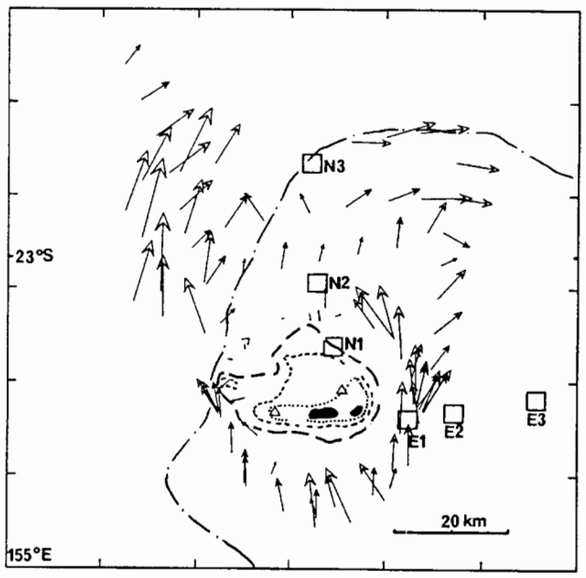

Fig. 1. Cato Reef, showing current vectors from the ADCP in the 49-m depth bin, using 20-min integrated profiles, during 15–16 February 1993 (P. Coutis and J. H. Middleton, personal communication). Maximum vector size is 74 cm s^{-1}. A northward flow averaging 30 cm s^{-1} is evident through the eastern transect, with flow disturbance to the north and north-north-west. Exposed reef is denoted in black, surrounded by the 50-m, 500-m, 1000-m and 2000-m isobaths. Δ, Anderaa current meter; □, plankton sampling stations.

Otolith Analyses

Each fish was measured (standard length, SL), then dried in a 60°C oven for 48 h and cooled in a desiccator for 30–60 min before being weighed on a Cahn electrobalance to the nearest 0·01 mg. Sagittal otoliths were extracted under polarized light, affixed to glass slides with fast-drying glue, and polished almost to the mid plane with fine-grade commercial sandpaper and 12-μm lapping film (Stevenson and Campana 1992). The otoliths were then soaked in water for 30 min, flipped, dried and glued with clear nail polish, then polished from the other side to the mid plane. The double-sided polish was necessary to penetrate the metamorphic zone (Gjøsæter 1987; Gartner 1991*a*), to expose the larval increments. Otoliths were examined with the ×100 and ×40 objectives of a microscope, and measured with the aid of a video system and digitizer connected to a Macintosh computer (Anderson and Moksness 1988).

In the rostral area (see Figs 2*b* and 2*c*), the widths of the marginal, incomplete increment and the last complete outer growth increment were measured, where possible, to the nearest 0·5 μm (see Table 2). All the recent growth increments of this region were then measured at the inner boundary of each discontinuous zone, and the otolith diameter through this region was recorded. The growth history was measured from the otolith core to the periphery, along a transect that was perpendicular to all increments (see Fig. 2*a*). Increments were measured on the TV monitor, coupled with direct viewing of the otolith in difficult regions (otolith core and metamorphic zone). Growth increments were counted two to three times along this transect in three stages: the larval zone, the metamorphic zone, and the postlarval zone.

RNA–DNA Analyses

Each fish was thawed, measured (standard length, anal body depth, and eye diameter), and freeze-dried over 24 h. Dried fish were then weighed to the nearest 0·01 mg on a Cahn electrobalance. Pelagic juveniles >16 mg dry weight (18 mm SL) were found to be too large for biochemical analysis and were excluded. Biochemical analysis involved a modified method of Berdalet and Dortch (1991) using the fluorochromes Hoechst 33258 (No. 382061, Calbiochem) and thiazole orange (T-1376, Coulter Electronics). The major modification was in the extraction procedure (Suthers *et al.* 1996). Larvae were thoroughly homogenized by hand in 10-mL Halfu homogenizing glass tubes with 1 mL ice-cold Tris–Ca^{2+} buffer and then sonicated for 30 s before being combined with the dyes. All materials were maintained on crushed ice.

Standard curves with single-strand calf thymus DNA Type I (D8899, Bioscientific) and baker's yeast RNA Type III (R7125, Bioscientific) were prepared and analysed daily. The working concentrations of Hoechst 33258 and thiazole orange were 3.5 μg mL^{-1} and 3 μg mL^{-1} respectively, made up in Tris–Ca^{2+} buffer. Fluorescence was recorded on a Perkin Elmer spectrophotometer set at excitation/emission wavelengths of 511/533 nm for thiazole orange and 350/460 nm for Hoechst 33258.

Statistical Analysis

To establish daily increment formation, the marginal (or peripheral) incomplete daily growth increment was converted to a percentage of the last complete growth increment. The percentage was calculated as $100*(W_n/W_{n-1})$, where W_n is the width of the marginal increment and W_{n-1} is the width of the last (complete) increment (Sepúlveda 1994).

Condition was compared between fish from E and N transects by analysis of covariance (ANCOVA). Residuals were then generated for each individual, by applying a common regression, after ensuring homogeneity of slopes between E and N transects.

RNA–DNA ratios were not used as the condition index for two reasons. Firstly, the ratio may be confounded because the concentration of RNA is derived from the concentration of DNA (Hovenkamp and Witte 1991; Suthers *et al.* 1996). Secondly, ratios may not entirely remove the effect of size (Packard and Boardman 1987). Therefore, the residuals of the regression of RNA on dry weight were generated as individual condition indices.

Results

The myctophid *Diaphus kapalae* (Nafpaktitis *et al.*, 1995), was found in the surface samples at all stations (Table 2). Very low numbers were captured at Station N1, which was always associated with a large biomass of macrozooplankton. Lengths ranged between 11–15 mm SL, with no trend in mean SL between the eastern and northern sides of the island (Table 2).

Otolith Analyses

The otolith morphology was similar to that described by Linkowski (1991), with an unambiguous larval zone of 38 increments radiating from a central primordium (CP), followed abruptly by a brown zone of 10–12 increments. This was followed equally abruptly by a post-metamorphic zone (Gjøsæter 1987; Gartner 1991*a*) of 3–16 clear, wide (~10 μm each) increments (Table 2, Fig. 2*a*).

In the brown zone, accessory primordia (APs) commenced at Day 38 after hatching (range Days 31–48) that within 10–20 μm formed continuous incremental structures around the periphery, parallel to the earlier larval growth rings (Figs 2*a* and 2*d*). The enumeration of these rings was difficult owing to persistent ring-splitting (Fig. 2*d*), which potentially halved the increment widths within a day. My interpretation of persistent ring-splitting in this zone (Fig. 2*d*) was based on assuming conservative otolith growth (Stevenson and Campana 1992) rather than sudden doubling of increment width at the beginning of the clear, outer increments. If this interpretation is incorrect, then all ages should be increased by 10–12 increments (about 17%).

The otolith core, bounded by the hatch check, was on average 8.2 μm in diameter (range 6–13 μm). After the first 4–6 narrow increments, growth in increment width

Table 2. Summary of otolith information collected and sample sizes (*N*) of *D. kapalae* at each station

SL, mean standard length (mm); DW, mean oven-dried weight (mg); N_{oto}, number of otoliths measured for marginal increments; N_{inc}, average number of post-larval increments measured for recent growth indices; L_{age}, average number of larval increments; T_{age}, average total number of increments; *G*, mean overall growth rate (mm) day^{-1}); N_{gh}, number of otoliths measured for complete growth history. Numbers in parentheses are standard errors

Station	N	SL	DW	N_{oto}	N_{inc}	L_{age}	T_{age}	G	N_{gh}
E1	17	13·6 (0·2)	5·65 (0·27)	15	9·6 (0·8)	40 (0.9)	60 (1.6)	0·228 (0·001)	11
E2	16	13·4 (0·1)	5·30 (0·18)	15	8·9 (0·5)	38 (0·8)	57 (1·0)	0·234 (0·005)	13
E3	9	13·1 (0·2)	5·42 (0·30)	7	8·0 (0·6)	37 (0·8)	56 (1·1)	0·234 (0·004)	6
N1	1	13·2	5·14	1	7·0	37	52	0·253	0
N2	42	13·2 (0·1)	5·21 (0·12)	36	6·9 (0·3)	39 (0·4)	57 (0·6)	0·233 (0·003)	24
N3	22	13·0 (0·1)	5·95 (0·26)	21	8·2 (0·7)	36 (0·7)	55 (1·1)	0·241 (0·005)	17
Total/mean	107	13·2 (0·1)	5·46 (0·09)	95	8·0 (0·3)	38 (0·3)	57 (0·5)	0·235 (0·002)	71

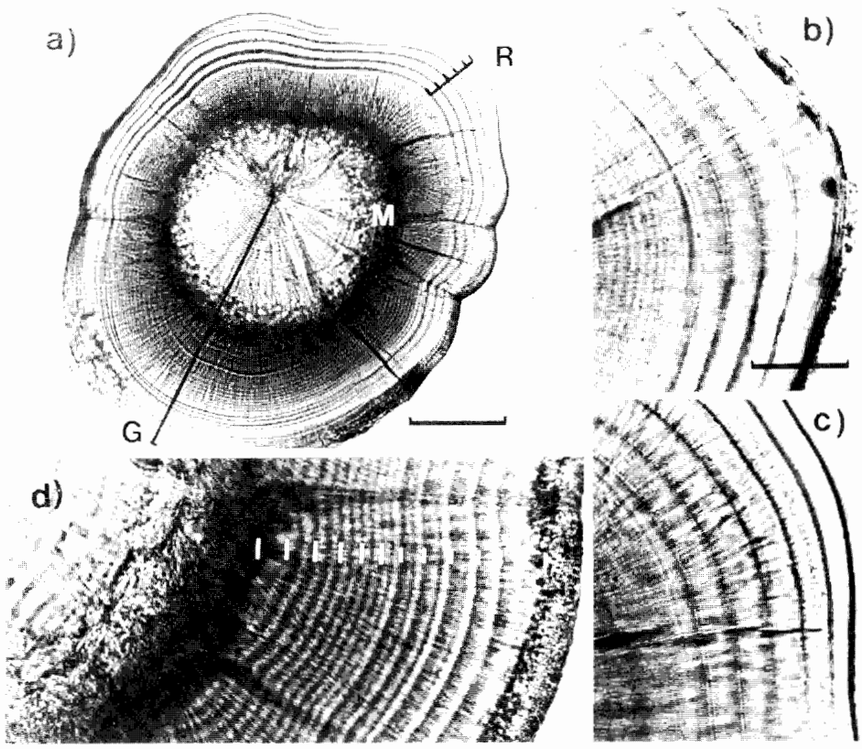

Fig. 2. *(a)* Lateral view of a polished sagitta from *Diaphus kapalae*, showing major landmarks and axes for measurement. G, growth history axis used in Fig. 3; M, beginning of metamorphic zone, starting with accessory primordia (area to the right of M is shown in Fig. 2*d*); R, rostrum of otolith, showing axis used for measuring. Scale bar, 100 μm. *(b)* Marginal increment formation in sagitta from a specimen caught at 1900 hours, with 22% of penultimate increment formed. Scale bar, 32 μm. *(c)* Marginal increment formation in sagitta from a specimen caught at 0100 hours, with 90% of penultimate increment formed. Scale same as in *b*. *(d)* Outer third of the sagitta in Fig. 2*a*, showing (from left to right) the larval growth increments, the formation of accessory primordia and the metamorphic zone (showing interpretation used in this study of ring structure, with larger marks in the metamorphic zone), and the outer growth increments of the post-metamorphic zone. Scale same as in *b*.

increased rapidly after 3 weeks until the beginning of the brown, metamorphic zone around Day 38 after hatching (Fig. 3). At Day 38, SL was on average 10.8 mm (range 8.4–11.6 mm), based on the range in radii at Increment 38: SL = 8.234 + 0.017*radius (n = 71, r^2 = 0.31). Ages ranged between 45 and 77 days after hatching, and overall growth rates were about 0.1 mm day^{-1} (Fig. 4).

Post-metamorphic Zone

There were 3–16 clear increments in the post-metamorphic zone (PMZ), which were easily measured in the rostrum region (Fig. 2*a*). Marginal increment analysis showed these PMZ increments to be formed daily. The width of the marginal increment, as a percentage of the penultimate increment, was linearly related to the time of sampling over the 8 h of complete darkness (Figs 2*b*, 2*c*, and 5). At 1900 hours, approximately 20% of the penultimate increment width was formed, including the narrower, dark, protein-rich discontinuous zone (Fig. 2*b*). By 0300 hours nearly 100% of the penultimate increment was formed, by completing the broader, white, translucent zone (Figs 2*c* and 5).

The width of recent growth increments in the rostrum area was used as an index of recent somatic growth, based on the linear relationship of the otolith diameter at the rostrum with SL (diameter = 66·67 + 36·51*SL, n = 98, r^2 = 0·31). Therefore, a change in the width of recent growth increment is proportionally equivalent to a change in SL.

The average width of the peripheral increments was linearly related to the total number of increments in the PMZ (Fig. 6*a*), excluding those larvae with <4 PMZ increments. Thus, on average, increment width increased over the first three PMZ increments before declining. By excluding fish with <4 PMZ increments, the average width

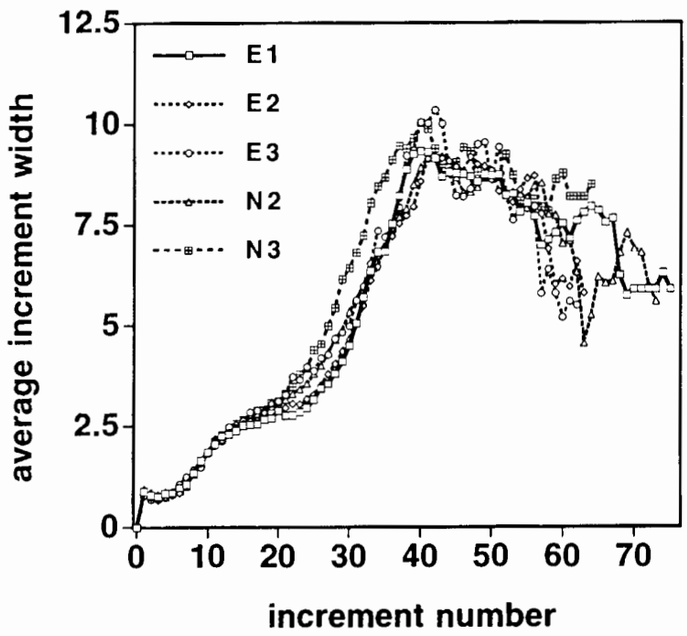

Fig. 3 Average increase in increment width (μm) in *D. kapalae* with respect to increment number (days) from hatching at each station.

of increments was linearly related to number of increments in the PMZ for Days 1 and 2 (n = 87, Fig. 6*a*), Days 3 and 4 (n = 81, Fig. 6*b*) and Days 5 and 6 (n = 53, Fig. 6*c*) before capture. There was no significant difference in slopes between the eastern and northern stations (ANCOVA, $P > 0.3$), but the intercepts were significantly greater by 0·8–1·3 μm in the northern stations for Days 1 and 2 and Days 3 and 4 (P = 0·001 and 0·05 respectively).

An individual residual-based index was generated from the overall regression on each day (Fig. 6), as the regression slopes between transects were found to be homogeneous. The non-linear section at <4 PMZ increments was excluded as noted in Fig. 6. Recent growth on Days 1 and 2 before capture was significantly greater at Station N3 than at Stations E1 and E2, and was significantly greater at Station E3 than that at E2 (1-way analysis of variance or ANOVA, Tukey's test, $P < 0.02$, Fig. 7*a*).

Recent growth on Days 3 and 4 before capture was the same at Stations E3 and N3 and significantly greater than at E1 and E2 (Tukey's test, $P < 0·02$, Fig. 7*b*). Recent growth on Days 5 and 6 before capture was not significantly different at any station (Fig. 7*c*, P = 0·49).

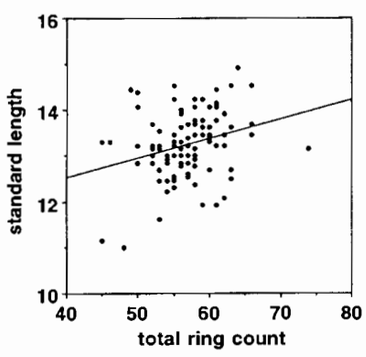

Fig. 4. Standard length (SL, mm) plotted against number of growth increments in *D. kapalae*. SL = 10·85 + 0·04*age (n = 95, r^2 = 0·08).

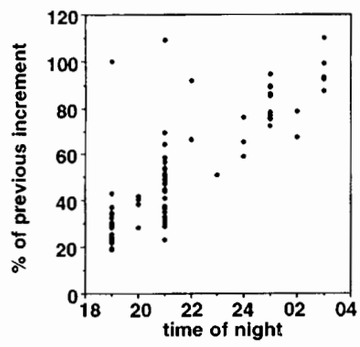

Fig. 5. Marginal increment formation in *D. kapalae* over 8 h from 1900 to 0300 hours, plotted as a percentage of the penultimate increment. Individuals are derived from all collections.

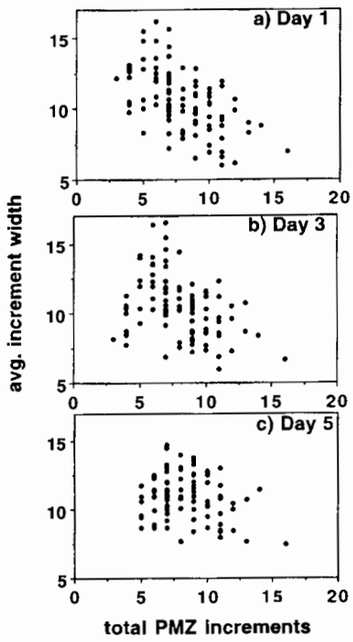

Fig. 6. Average width (μm) of increments plotted against the number of outer, postlarval growth increments. *(a)* Days 1 and 2 before capture: width = 14·41 – 0·49*increments, n = 87, r^2 = 0·31, for total PMZ increments <4. *(b)* Days 3 and 4 before capture = 15·70 – 0·59*increments, n = 81, r^2 = 0·31, for total PMZ increments <6. *(c)* Days 5 and 6 before capture: width = 15·28 – 0·45*increments, n = 53, r^2 = 0·19, for total PMZ increments <8.

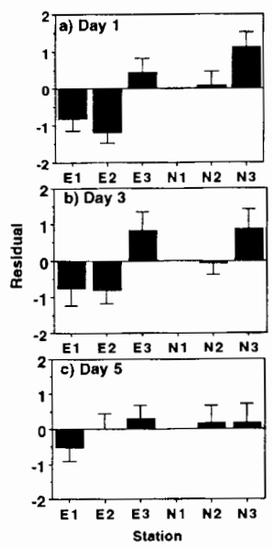

Fig. 7. Recent growth indices, derived from the residuals of Fig. 6 and excluding the non-linear portion of *(a)* Days 1 and 2 (increments <4), *(b)* Days 3 and 4 (increments <6), and *(c)* Days 5 and 6 (increments <8). The one fish from Station N1 was excluded. Error bars are standard error.

The recent otolith growth on Days 1 and 2 before capture was significantly correlated to the zooplankton biomass, as determined by the OPC, in the medium size range (1000–2500 μm equivalent spherical diameter, r = 0·78, Fig. 8), as it also was on Days 3 and 4 (r = 0·70). Greater concentrations of medium-sized particles tended to occur at the N stations (Fig. 8). There was no significant correlation on Days 5 and 6 (r = 0·10). Recent growth was not correlated to the concentration of small particles (300–1000 μm esd).

RNA–Dry Weight

The average sizes of *Diaphus kapalae* used in the RNA–DNA analysis were similar to the average sizes used for otolith analyses (within 2·6 mm SL, Tables 2 and 3). The average RNA:DNA ratio at each station ranged between 0·51 and 0·60 (except the one individual at N1) and showed no trend within or between transects (Table 3). The amount of RNA was related to DNA by: RNA = 28·04 + 0·27*DNA, n = 62, r^2 = 0·21.

Fish from the northern stations had significantly more RNA per milligram of dry weight than did those from the eastern stations (ANCOVA: slopes, P > 0·6; intercepts, P = 0·04). Therefore, a common regression was fitted (Fig. 9), and the residuals from this relationship were used as individual condition indices and to calculate station averages. The average RNA–DW index of fish was significantly greater at Station N3 than at Station E3 (Tukey's test, P = 0·02), whereas the other comparisons were not significantly different (ANOVA, P > 0·18, Fig. 10). In contrast to the otolith index, the mean RNA–DW index for each sample showed no significant relationship to the concentration of medium-sized particles (r = 0·04).

The biochemical and otolith indices on Days 1 and 2 (derived for separate individuals from the same sample) for

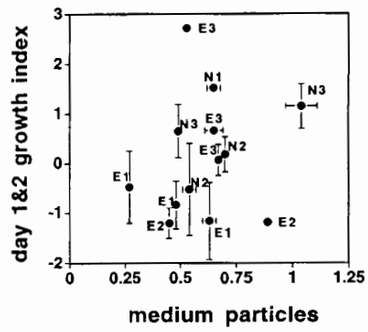

Fig. 8. Average recent growth index on Days 1 and 2 before capture for all stations and nights plotted against zooplankton biomass recorded with the optical plankton counter in the medium size range (1000–2500 μm, number per 10 L, r = 0·78). Station labels on different nights are beside each data point. Error bars are standard error.

Table 3. Summary of RNA–DNA information used for *D. kapalae*
n, sample size; SL, mean standard length (mm); DW, mean freeze-dried weight (mg); RNA/DNA, mean ratio. Numbers in parentheses are standard errors

Station	*n*	SL	DW	RNA/DNA
E1	11	13·7 (0·2)	7·6 (0·3)	0·60 (0·04)
E2	12	14·6 (0·5)	7·6 (0·9)	0·54 (0·04)
E3	6	14·1 (0·7)	7·5 (0·8)	0·51 (0·08)
N1	1	15·8	8·2	0·39
N2	17	13·9 (0·3)	7·0 (0·5)	0·59 (0·04)
N3	15	15·1 (0·3)	8·7 (0·6)	0·59 (0·05)

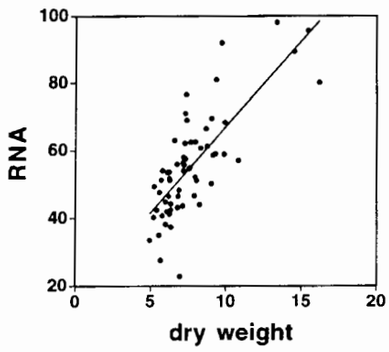

Fig. 9. Relationship of RNA (μg per fish) to dry weight (DW, mg) for *D. kapalae* (RNA = 16·23 + 5·08*DW, $n = 62$, $r^2 = 0{\cdot}59$).

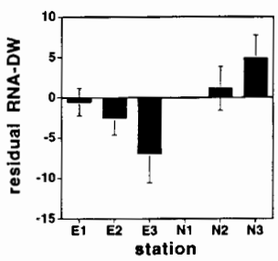

Fig. 10. Average residuals from the regression of RNA on dry weight (DW) (Fig. 9) for each station for *D. kapalae*. The one fish from Station N1 was excluded. Error bars are standard error.

each station × night sample were significantly correlated (weighted correlation, $r = 0{\cdot}39$, Fig. 11). Two obvious outlier samples had one fish each (Fig. 11), and if these were excluded, the correlation coefficient increased to 0·66. The relationship was still significant and positive for the otolith index on Days 3 and 4, but by Days 5 and 6 there was no trend.

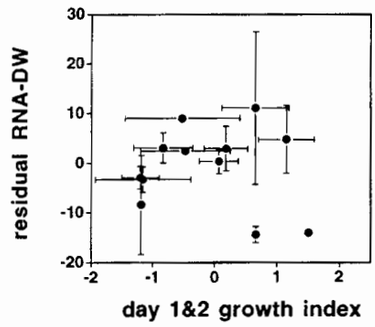

Fig. 11. Scatterplot of mean residual RNA on dry weight (DW) for *D. kapalae* for each replicate night at all stations, on mean residual otolith growth on Days 1 and 2 before capture. Error bars are standard error.

Discussion

Overall, *D. kapalae* showed significantly greater recent otolith growth and greater RNA per milligram of dry weight at the furthest downstream station (N3) than at most of the free stream stations (E1–E3). Importantly, the recent growth index was correlated with the concentration of medium-sized particles (Fig. 8), these being the size fraction appropriate for pelagic juveniles of 10–15 mm SL. This assumes that the zooplankton conditions recorded by the OPC between 5 and 25 m depth were those experienced by the larvae over the previous two days. In general, smaller myctophids tend to persist in the 25–75 m depth range (Hopkins and Gartner 1992). Although higher recent growth was correlated with higher microzooplankton at the northern stations, the greatest abundance of macrozooplankton found in the net was at Station N1, where very few larvae were present. The higher biomass in the region of flow disturbance is probably due to convergence and aggregation rather than to enhanced production, because current flow had temporarily reversed during the previous week (discussed below).

Recent growth in pelagic juvenile cod off eastern Canada also exhibited higher correlation with the largest size fraction (>1050 μm) than with the smaller size fractions (Suthers *et al.* 1989). Bailey (1989) also observed significant correlations between recent otolith growth and zooplankton biomass in pelagic juvenile walleye pollock.

Intercomparison of RNA and Otolith Growth Indices

The concentrations of RNA found in *D. kapalae* are much lower than those previously reported (e.g. Westerman and Holt 1994). Although the present technique uses a different procedure and dye, freeze-drying is unlikely to have affected RNA yields, as many other studies also freeze-dry samples before analysis (e.g. Buckley and Lough 1987; Malloy and Targett 1994). Most other studies of RNA

condition are conducted at temperatures much lower than that recorded here (25°C) and in larvae rather than pelagic juveniles. Malloy and Targett (1994) state that RNA measures of juvenile summer flounder are much lower and less responsive to growth rates at temperatures >25°C, partly because of increased turnover rates of ribosomes and enzymes. Hence, the RNA concentrations in *D. kapalae* are probably consistent with slow-growing pelagic juveniles (0·1 mm day^{-1}, Fig. 4; Gartner 1991*a*) in tropical oligotrophic waters with nutrients at or below detectable limits.

Biochemical and otolith analyses were conducted on pelagic juveniles from the same net tow, but not on the same individuals. Consequently, any comparison between the two measures (Fig. 11) assumes that the two analyses reflect, on average, similar larvae from the same oceanographic conditions. The validity of this assumption probably declines with greater intervals before capture. The RNA–dry weight index was positively correlated with the recent growth index over Days 1 and 2 and Days 3 and 4 before capture, but the correlation was not significant at Days 5 and 6. In general, RNA indices reflect conditions over the previous day (Martin and Wright 1987). An interesting exception was the very low RNA–DW index at Station E3 (Fig. 10), relative to the above-average otolith index at E3, particularly at Days 3 and 4 (Fig. 7). The fish at E3 appear to be in declining condition owing to temporal variation in the wake, and the otolith index may be less responsive than are RNA concentrations.

Other studies that have examined otolith and RNA indices (Hovenkamp 1990; Hovenkamp and Witte 1991; both also not of the same individuals) show that RNA and otolith condition are consistently correlated. Otolith and biochemical analyses of the same individuals are possible (e.g. Suthers *et al.* 1992) and should be further examined.

Relationship of Condition to Current Flow

Anderaa current meters were deployed from October 1992 to February 1993 at two locations on Cato Reef along the 50-m isobath (P. Coutis and J. H. Middleton, personal communication). Daily current records were predominantly to the north at 30 cm s^{-1} during most of January 1993 and particularly during the 4–5 days before biological sampling. At 5–10 days before sampling, however, currents exhibited some significant reversals to the south (possibly associated with Cyclone Oliver near Wreck Reef, 130 km north-north-east). The current-meter data are consistent with the recent otolith growth index, which showed that by Days 5 and 6 before capture there was no significant difference between any of the stations.

The physical data enable interpretation of another apparent anomaly in the condition data. Otolith and RNA indices showed that condition at Station N2 was not significantly different from the overall average condition (Figs 7 and 10), with greater condition at N3. Modelled steady-current flow reveals an anticyclonic eddy north-west of Cato Reef, with a residence time of about two weeks (P. Coutis, personal communication), and this is apparent in the ADCP flow at 50 m (Fig. 1). Station N2 could have received an influx of poor-condition larvae from Station E1 that may have reduced the overall average.

Life-history Information of D. kapalae

The broad, white continuous zone of outer growth increments was formed in the surface waters during darkness between 1900 and 0400 hours, whereas the narrower, brown discontinuous zone appears to have formed during daylight, presumably at depth (Fig. 5). Thus, one complete increment is assumed to form every 24 h. Although individuals were sampled only over 8 out of 24 hours, this conclusion is identical to that of Gartner (1991*a*), who sampled three species of myctophids over the full 24 h. No pelagic juvenile myctophids were captured during the present daylight sampling, from the surface to 120 m.

The brown (metamorphic) zone of the otolith (Fig. 2) has been argued as representing a shift between the larval habitat (surface waters) and the sub-adult habitat (>200 m, Gjøsæter 1987; Gartner 1991*a*). Linkowski (1991) suggests that the formation of accessory primordia (APs) at the beginning of this zone does not necessarily correspond to metamorphosis, as APs were observed in this genus before size at transformation (reported to occur around 11·5 mm SL). Similarly, in the present study APs were calculated to occur at about 10·8 mm SL. APs occur when the axis of growth shifts from being centred about the central primordium to being centred about the accessory primordia and is probably associated with a change in habitat and the development of increasing diel vertical migration.

Incremental growth was observed to occur in the surface waters at night, supporting Gartner's (1991*b*) conclusion that myctophids are ecologically epipelagic rather than mesopelagic. The larval duration of *D. kapalae* was about 38 days, which is at the upper end of the range for nine myctophids reported to have larval durations of 26–40 days (Gjøsæter 1987; Gartner 1991*b*).

Biological Significance of Flow Disturbance about an Island

The effects of flow disturbance on pelagic juvenile condition are complex, including the shape and stability of the eddies downstream (e.g. Cowen and Castro 1994), current flow the previous week, possible mixing of starving and feeding individuals, possible trophic lag effects, and predation. The potentially confounding influence of island runoff is not possible around a small, low-relief island such as Cato. However, the spatial/temporal scales of observation

(*sensu* Le Borgne *et al.* 1985) and the temporal stability of flow disturbance (over at least 4–5 days) can influence the detection of an effect. Nevertheless, a rapid effect on fish condition may be expected in larval and pelagic juvenile fish that exist in an otherwise oligotrophic ocean. The response in condition around Cato Reef occurred over a few days. Two independently derived correlated indices showed that condition was significantly enhanced at a station 38 km downstream. This increase in myctophid condition is probably derived from aggregation and trapping of zooplankton rather than any increase in production (Rogers 1994), owing to current variation observed during the previous week. Myctophids and other mesopelagic fish form an important component of the diet in larger predatory fishes (Rogers 1994). The significance of flow disturbance to fishery production is the next important step.

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