Onshore-offshore distribution and abundance of tuna larvae (Pisces: Scombridae: Thunnini) in near-reef waters of the Coral Sea

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Abstract—The on-offshore distributions of tuna larvae in near-reef waters of the Coral Sea, near Lizard Island (14°30′S, 145°27′E), Australia, were investigated during four cruises from November 1984 to February 1985 to test the hypothesis that larvae of these oceanic fishes are found in highest abundance near coral reefs. Oblique bongo net tows were made in five on-offshore blocks in the Coral Sea, ranging from 0–18.5 km offshore of the outer reefs of the Great Barrier Reef, as well as inside the Great Barrier Reef Lagoon. The smallest individuals (<3.2 mm SL) of the genus *Thunnus* could not be identified to species, and are referred to as *Thunnus* spp. We found species-specific distributional patterns. *Thunnus* spp. and *T. alalunga* (albacore) larvae were most abundant (up to 68 larvae/100 m^2) in near-reef (0–5.5 km offshore) waters, whereas *Katsuwonus pelamis* (skipjack tuna) larvae increased in abundance in the offshore direction (up to 228 larvae/100 m^2, 11.1–18.5 km offshore). Larvae of *T. albacares* (yellowfin tuna) and *Euthynnus affinis* (kawakawa) were relatively rare throughout the study region, and the patterns of their distributions were inconclusive. Few larvae of any tuna species were found in the lagoon. Size-frequency distributions revealed a greater proportion of small larvae inshore compared to offshore for *K. pelamis* and *T. albacares*. The absence of significant differences in size-frequency distributions for other species and during the other cruises was most likely due to the low numbers of larvae. Larval distributions probably resulted from a combination of patterns of spawning and vertical distribution, combined with wind-driven onshore advection and downwelling on the seaward side of the outer reefs.

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Large-scale (100s km) distributions of tuna larvae (family Scombridae), particularly of the commercially important genera *Thunnus* and *Katsuwonus*, have been extensively investigated because of the need to identify spawning locations and the possibility of estimating spawning stock biomass from surveys of larvae (Strasburg, 1960; Richards, 1976; Scott et al., 1993). Despite this effort, and the apparent abundance and fecundity of *T. albacares* (yellowfin tuna) and *K. pelamis* (skipjack tuna) in the western and central Pacific Ocean, relatively low mean concentrations (2–4 larvae/100 m^3, Leis et al., 1991) and abundances of tuna larvae (2–8 larvae/10 m^2, Leis et al., 1991) have been found during most sampling programs. Low numbers of tuna larvae in any one site or region may simply reflect a broadly distributed, but sparse, spawning pattern of adults, as indicated by the wide geographical ranges of *T. albacares* and *K. pelamis* larvae. Other possible explanations, however, are that previous sampling scales of 100s km between samples were too coarse to account for spatial variability in abundances (Davis et al., 1990a), and that tuna larvae are more abundant in undersampled near-reef areas (Leis et al., 1991).

Nearly all sampling of tuna larvae has been conducted in the open ocean because of the oceanic distributions of adults; however relatively high concentrations of tuna larvae have been found in previously undersampled tropical near-reef (<5 km offshore) locations in three studies (Miller, 1979; Leis et al., 1991; Boehlert and Mundy, 1994). Concentrations of larval *T. albacares* were up to two orders of magnitude greater within 2 km of leeward (west) Oahu Island, Hawaii, than published concentrations in surrounding oceanic waters (Miller, 1979), and *Thunnus* spp. and *K. pelamis* larvae were up to 100 times more concentrated within 200 m of coral reefs in French Polynesia than in oceanic waters of the central Pacific Ocean (Leis et al., 1991). Because adjacent oceanic locations were not simultaneously sampled in these near-reef studies, a direct comparison of these two habitats was not possible. Furthermore, comparisons between the near-reef values of larval tuna concentration determined by Miller (1979) and Leis et al. (1991), and those determined for oceanic habitats in the central Pacific Ocean in other studies, may also be confounded because of differences in sampling methods employed between the two

habitats. Near-reef concentrations were determined by using short (<15 min.) horizontal tows at or near the surface (Miller, 1979; Leis et al., 1991), whereas oceanic sampling in the region has generally involved tows of longer duration (≥30 min.), with nets towed either horizontally at the surface or obliquely from depths reaching 200 m (Matsumoto, 1958; Nakamura and Matsumoto, 1966). Because distributions of tuna larvae are vertically stratified, and *Thunnus* spp. larvae are rarely found at depths greater than 50 m (Davis et al., 1990b; Boehlert and Mundy, 1994), oblique tows to depths in excess of 100 m most likely underestimate concentrations in shallower strata. Because of this situation, it is appropriate to use the measure of abundance (i.e., the number of larvae below a standard surface area of water) rather than concentration (numbers of larvae per standard volume) to compare numbers of larvae among sites where tows were taken to different depths.

Abundances of tuna larvae were determined at both near-reef (2 km offshore) and oceanic sites (~30 km offshore) around the Hawaiian island of Oahu by Boehlert and Mundy (1994) by oblique sampling to 200 m depth. The abundance of *Thunnus* spp. larvae decreased with increasing distance offshore, but only on the leeward side of Oahu Island. Interestingly, the abundance of *K. pelamis* larvae actually increased with distance from the reef on both sides of the island (Boehlert and Mundy, 1994), indicating the possibility of important taxa-specific differences in near-reef distributions of tuna larvae.

The possibility that tuna larvae are generally concentrated near islands and reefs, and not in the open ocean, has important implications for the protection of these vulnerable life stages. Large numbers of tuna larvae near shore have been found in only two regions in the central Pacific Ocean, and only near oceanic islands; therefore further investigation of the generality of this phenomenon is required. Considering that patches of highly concentrated (10,945 larvae/500 m^3) *T. maccoyii* (southern bluefin tuna) larvae in the North East Indian Ocean were only 5–15 km in diameter (Davis et al., 1990a), further investigation of fine-scale patterns of larval tuna distribution is also warranted.

The aim of the present study was to investigate the near-reef abundance and on-offshore distributions of tuna larvae in the Coral Sea, near the Great Barrier Reef, Australia, over a fine (1–10 km) scale. Although the sampling design was originally intended for investigation of distributions of reef fish larvae (Leis, 1986; Leis and Reader, 1991), the sampling scale and gradation of habitat from near-reef to oceanic in the offshore direction also made it appropriate for investigating the near-reef distributions of tuna larvae.

Materials and methods

Study area and experimental design

Larval fish samples were collected in an area of the Coral Sea between Lizard Island (14°30′S, 145°27′E) and 19 km seaward of the outer ribbon reefs of the Great Barrier Reef, Australia (Fig. 1). Lizard Island is situated approximately halfway across the Great Barrier Reef Lagoon (hereafter "lagoon") where water depths range from 25 to 40 m. The outer reefs lie on the continental shelf break, beyond which depth increases rapidly reaching 2000 m within 12 km. There is an abrupt change from shallow, protected waters of the lagoon to oceanic conditions in the offshore direction. Winds were usually from the E to SE during the study period (common for this region); therefore the near-reef waters that we sampled were on the windward side of the outer reefs.

Four cruises were conducted to investigate the horizontal distribution of fish larvae: 1) 2–5 November 1984 (early November cruise), 2) 17 and 20–22 November 1984 (late November cruise), 3) 30 January–2 February 1985 (early February cruise), and 4) 9–13 February 1985 (late February cruise). On each cruise, six samples were taken in each of five on-offshore blocks defined by distance (nautical miles, nmi) from the outer reef crest: A) 0–0.25 nmi (0–0.46 km), B) 0.25–1.0 nmi (0.46–1.85 km), C) 1.0–3.0 nmi (1.85–5.56 km), D) 3.0–6.0 nmi (5.56–11.1 km), and E) 6.0–10.0 nmi (11.1–18.5 km, Fig. 1). On each cruise, six samples were also taken in the lagoon between Lizard Island and the outer reefs (Fig. 1). Samples were taken over four consecutive days on each cruise. Offshore transects were planned to be conducted over three days, and two samples to be taken in each block at randomly chosen distances from the reef on each day. All samples in the lagoon were taken on the same day. Transects were centered on a different reef each day and were started from opposite ends on alternate days. Distance from the reef was determined by radar reflection off the waves breaking on the outer reef crest. Because of this method of measurement, actual distance from the reef varied by approximately 100 m depending on the tide and sea state. Because of bad weather on the second cruise, two days elapsed between the sampling of lagoon and offshore waters, and only two samples could be taken in block A. Offshore transects were conducted over four days during the fourth cruise because of mechanical problems.

Sampling procedure

Quantitative, double-oblique plankton tows were made from a 14-m catamaran with a bongo net (cylinder-cone mesh design) with 0.85 m mouth diameter and 0.5-mm mesh. The net was towed at approximately 1 m/s and was fitted with both a calibrated mechanical flowmeter and a calibrated mechanical depth and distance recorder. Tows usually filtered 1000–2000 m^3 of water with a mean volume (and standard deviation) of 1554 (585), 1644 (629), 1637 (306), and 1348 (278) m^3 for each cruise, respectively. All tows were completed during daylight, between one hour after sunrise and one hour before sunset. Tows were taken to a target depth of 200 m on the first cruise and to 120 m thereafter, except in the lagoon and block A where they were taken as close to the bottom as considered safe. The net hit bottom

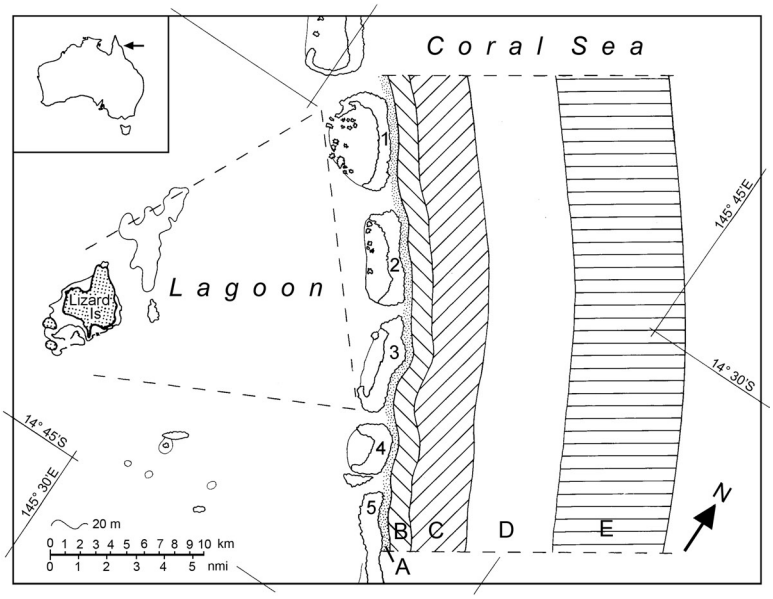

Figure 1

Map of the study area in the Great Barrier Reef Lagoon and Coral Sea, near Lizard Island, Australia. Lagoon samples were taken between Lizard Island and the outer barrier reefs, within the boundaries indicated by dashed lines. Offshore samples were taken in five blocks, A–E, in the Coral Sea. The outer reefs are 1) Day, 2) Carter, 3) Yonge, 4) No Name, and 5) Number 10 Ribbon. Map adapted from Leis et al. (1987).

occasionally in block A because of great variation in water depth in this area. Samples were fixed in formalin (5–10% in seawater) in the field.

Laboratory procedure

Larvae from both the port and starboard sides of the bongo net were sorted, except for those in the lagoon samples from the first and second cruises where the catch from only one randomly chosen side was sorted because of high plankton volumes. Samples from block D were not sorted because of funding cuts to the research program. Larvae were removed with the aid of a dissecting microscope and transferred to 70% ethanol for storage. Tuna larvae (family Scombridae) were identified to species, when possible, by using the descriptions of Fritzsche (1978) and Nishikawa and Rimmer (1987). Larvae of *T. albacares* and *T. alalunga* (albacore) <3.2 mm standard length (SL) could not be separated and were identified as *Thunnus* spp. larvae. For larger larvae, Richards et al. (1990) advocate also using an osteological character, rather than relying solely on pigment, when identifying *Thunnus* larvae to species. However, their study was primarily concerned with *T. atlanticus* (blackfin tuna), a species that is not found in our study area. Further, the osteological character in *T. alalunga* and *T. albacares* seems to vary about as much as does the pigment character, and the former cannot be used in specimens <6 mm SL (Richards et al., 1990). Therefore, we relied on the pigment character to separate our *T. alalunga* and *T. albacares* larvae ≥3.2 mm SL. We note, however, that one-third of the *Thunnus* larvae >6 mm SL that we cleared and stained had pigment inconsistent with the osteological characters listed in Table 1 of Richards et al. (1990). Therefore, according to the criteria of Richards et al. (1990, Table 1), at least 67% of our *Thunnus* larvae are correctly identified to species, and between 0 and 33% may be misidentified to species. Given the variability in osteological features noted by Richards et al. (1990, their Tables 2 and 3), we cannot be more precise about this "uncertain" 33%. Larvae of the genus *Auxis* cannot currently be identified to species (Nishikawa and Rimmer, 1987), and adults of both *A. thazard* (frigate tuna) and *A. rochei* (bullet tuna) inhabit the region of the study area (Collette and Nauen, 1983). *Auxis* larvae were therefore all identified as *Auxis* spp. Larvae of *Auxis* spp. and *Euthynnus affinis* (kawakawa) <2.3 mm SL could not be separated and were identified as *Auxis-Euthynnus* larvae. Notochord length and SL were measured to the nearest 0.1 mm for preflexion and postflexion larvae, respectively, by using a calibrated ocular micrometer. No correction was made for shrinkage of the larvae.

Statistical analyses

Abundances (no. of larvae/100 m^2) were calculated by 1) calculating larval concentration (larvae/m^3), 2) multiplying concentration by the depth (m) sampled, and 3) multiplying the result by 100 to obtain appro-

Table 1

Species composition of tuna larvae (family Scombridae) caught during four cruises in the Coral Sea, near the Great Barrier Reef, between November 1984 and February 1985. Values are numbers of larvae caught. Taxa are ordered to allow comparison of larval numbers among groups comprising the same genera.

Taxon	Early November cruise	Late November cruise	Early February cruise	Late February cruise	Species total	Proportion of total catch (%)
Katsuwonus pelamis	55	89	109	94	347	34
Thunnus spp.	3	24	116	29	172	17
Thunnus albacares	11	19	49	16	95	9
Thunnus alalunga	69	62	26	14	171	17
Auxis-Euthynnus	13	2	72	9	96	10
Euthynnus affinis	49	4	54	1	108	11
Auxis spp.	5	0	10	7	22	2
Total	205	200	436	170	1011	

priately scaled values. Abundance values incorporate a depth component, and are therefore appropriate for comparing oblique samples taken down to different depths. Statistical analyses of on-offshore patterns of distribution of tuna larvae were performed on natural log-transformed abundances, following inspection of the data for normality and heterogeneity of variance. A count of 1 was added to all data-points before transformation, to allow transformation of zero values. Preflexion and postflexion larvae were combined for on-offshore analyses. For each taxon, analysis was done only for cruises with an average larval abundance >1 larvae/100 m^2 to avoid problems associated with numerous zeros. Lagoon samples were not included in calculation of the cruise average because few larvae of any tuna taxon were caught in the lagoon. Only *K. pelamis* larvae were sufficiently abundant for analysis on all four cruises, and their abundance among on-offshore blocks (including the lagoon) and cruises was compared by using a two-factor analysis of variance (ANOVA). For other taxa, abundance among blocks was analyzed with a one-factor ANOVA for each cruise with larval abundance >1 larvae/100m^2. When ANOVA tests yielded significant (P<0.05) results, pairwise differences between blocks were analyzed using Tukey's test. *Auxis* spp. larvae were not sufficiently abundant on any cruise to allow for statistical analysis.

Size-frequency data from blocks A and B (inshore zone, 0–1.85 km from the reef) were pooled and compared with size-frequency data pooled from blocks C and E (offshore zone, >1.85 km from the reef) using the Kolmogorov-Smirnov (K-S) test. Data were pooled to increase n, because few taxa had sufficient numbers of larvae in each block to provide adequate statistical power. K-S tests were done on data from individual cruises. Larvae from the lagoon were excluded from size-frequency analysis because of low abundance. The significance level used for all statistical tests was 0.05. Not enough *E. affinis* larvae were caught in both zones on any cruise to allow a statistical comparison of size distributions.

Results

Species composition and abundance

Over 1000 tuna larvae were caught, comprising at least five species and four genera (Table 1). Larvae of *K. pelamis* were the most abundant, making up over one third of all tuna larvae caught. Numerous small (<3.2 mm SL) *Thunnus* spp. larvae were caught on the early February cruise, coinciding with a peak in abundance of less common *T. albacares* larvae. In contrast, *T. alalunga* larvae were most abundant on the November cruises, and only 26 individuals were caught on the early February cruise. It is, therefore, likely that most of the *Thunnus* spp. larvae were *T. albacares*. Larvae of other *Thunnus* species (e.g., *T. obesus* [bigeye tuna] or *T. tonggol* [longtail tuna]) were not caught and would have been distinguishable from *T. albacares* and *T. alalunga*, even at small (<3.2 mm SL) sizes (Fritzsche, 1978). *Euthynnus affinis* larvae were most common on the early November and early February cruises, and *Auxis-Euthynnus* larvae were most abundant on the early February cruise. Only 22 *Auxis* spp. larvae were caught during the study, therefore *Auxis-Euthynnus* larvae were most likely primarily *E. affinis* larvae.

On-offshore distribution

Tuna larvae generally had near-reef distributions, as greatest abundances usually occurred within 5.6 km of the outer reefs of the Great Barrier Reef in the Coral Sea. Patterns of on-offshore distribution differed among taxa, however.

Species of *Thunnus* had the most consistent near-reef distribution among the taxa of tuna larvae, with

highest abundances found within 5.6 km of the outer reefs on most cruises with sufficient numbers of larvae for statistical analysis. *Thunnus* spp. larvae were more abundant in block C than in either the lagoon or block E on the late November cruise (Tukey's test, $P<0.01$, Fig. 2) (blocks A and B being intermediate), and more abundant in blocks A and B than in the three other blocks, which did not differ, on the early February cruise (Tukey's test, $P<0.03$, Fig. 2). *Thunnus* spp. larvae showed a similar inshore distribution on the late February cruise; however the only significant difference was a greater abundance of larvae in block B than in the lagoon (Tukey's Test, $P<0.03$, Fig. 2). *Thunnus alalunga* larvae were more abundant in blocks B and C than in the lagoon on the early November cruise (Tukey's test, $P<0.02$, Fig. 3) (the the other blocks being intermediate) and more abundant in block A than in either the lagoon or block E on the early February cruise (Tukey's test, $P<0.04$, Fig. 3). A similar pattern of abundance of *T. alalunga* larvae occurred on the late November cruise; however differences among blocks were not quite significant (Tukey's test, $P=0.051$, Fig. 3). *Thunnus albacares* larvae were most abundant in block A on the early February cruise; however there were no significant differences among blocks (ANOVA, $P=0.06$, Fig. 4).

Distributions of *E. affinis* larvae and *Auxis-Euthynnus* larvae were similar to that of *T. alalunga*, and appeared to be most abundant within 5.6 km of the outer reefs. Differences in larval abundance among blocks were not, however, significant for the early November (ANOVA, $P=0.14$, Fig. 5) and early February (ANOVA $P=0.11$, Fig. 5) cruises analyzed for *E. affinis*, or the early February (ANOVA, $P=0.06$, Fig. 5) cruise analyzed for *Auxis-Euthynnus*.

In contrast to other tuna taxa, the abundance of *K. pelamis* larvae increased in the offshore direction. Despite a significant interaction among blocks and cruises (ANOVA, $P=0.004$), *K. pelamis* larvae were more abundant in block E than in blocks A, B, and the lagoon on the early November cruise (Tukey's test, $P<0.02$, Fig. 6), more abundant in blocks C and E than in the lagoon on the early February cruise (Tukey's test, $P<0.002$, Fig. 6), and more abundant in block E than the lagoon on the late February cruise (Tukey's test, $P<0.05$, Fig. 6). The statistical interaction among blocks and cruises was most likely caused by a relatively great abundance (mean 12.1 larvae/100 m^2) of *K. pelamis* larvae in the lagoon on the late November cruise, compared with abundance in the lagoon on the early November, early February, and late February cruises (means 0.6, 0.0, and 3.5 larvae/100 m^2, respectively, Fig. 6). Apart from *K. pelamis* and *T. alalunga* larvae on the late November cruise, few larvae of any tuna taxon were found in the lagoon.

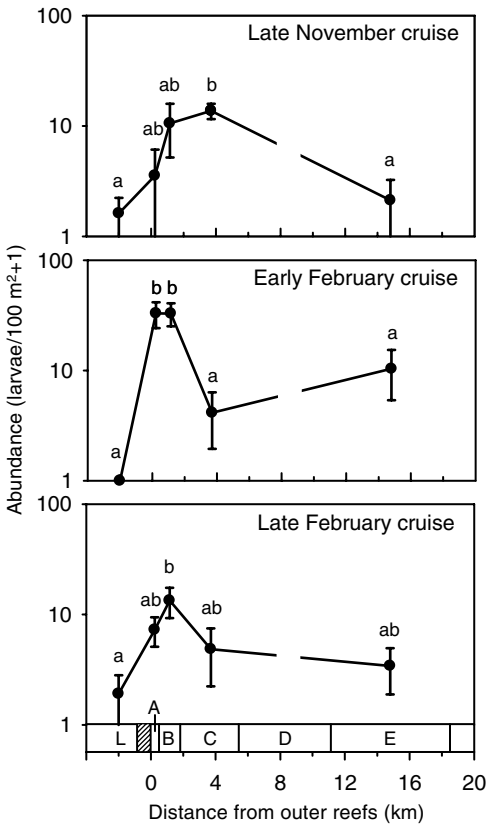

Figure 2

Mean abundance (larvae/100 m^2+1 [± standard error]) of *Thunnus* spp. larvae with distance from the outer reefs of the Great Barrier Reef during the late November, early February, and late February cruises in the Coral Sea. Data points indicate the midpoint of sampling blocks (A–E) by distance, except for the Great Barrier Reef Lagoon (L on the *x* axis), the display of which is categorical and does not reflect the true distance from the other blocks. The *y* axis is $\log_{10}$ scale. The *x* axis shows the width of each sampling block (km). The hatched area on the *x* axis indicates the position of the outer reef area of the Great Barrier Reef. Within a cruise, if data points share a lowercase letter, they were not significantly different from each other according to Tukey's *post hoc* test. Abundance data was not obtained for block D.

Size-frequency distribution

Tuna larvae ranged in size from 1.7 to 15 mm SL; however most taxa had a strong size mode at 2–4 mm SL. For all species, larvae were of similar size on each cruise, which were at least seven days apart.

Differences in size-frequency distributions of larvae between inshore and offshore zones of the Coral Sea were taxa-specific, however for those tuna taxa where significant differences were detected, there was a greater proportion of small larvae in the inshore zone. A greater proportion of small (2–3.5 mm SL) *K. pelamis* larvae was found in the inshore zone, compared with the offshore zone, on both the early February

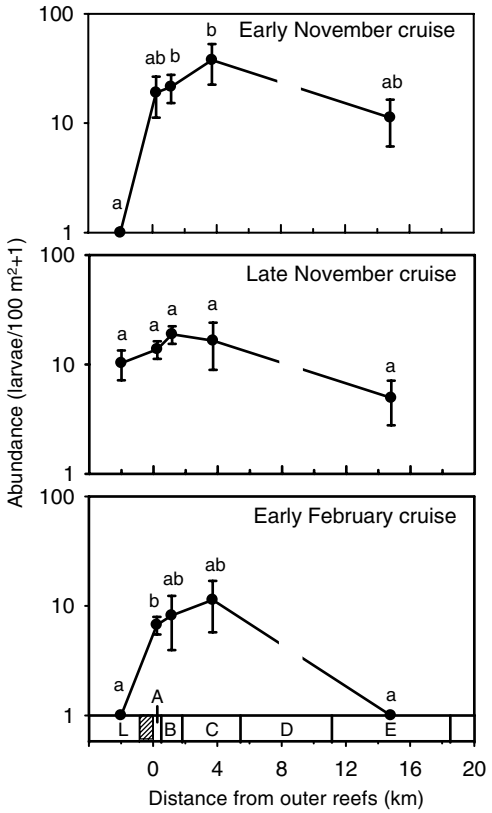

Figure 3

Mean abundance (larvae/100 m^2+1 [± standard error]) of *Thunnus alalunga* (albacore) larvae with distance from the outer reefs of the Great Barrier Reef during the early November, late November, and early February cruises in the Coral Sea. Data points indicate the midpoint of sampling blocks (A–E) by distance, except for the Great Barrier Reef Lagoon (L on the *x* axis) the display of which is categorical and does not reflect the true distance from the other blocks. The *y* axis is $\log_{10}$ scale. The *x* axis shows the width of each sampling block (km). The hatched area on the *x* axis indicates the position of the outer reef area of the Great Barrier Reef. Within a cruise, if data points share a lowercase letter, they were not significantly different from each other according to Tukey's *post hoc* test. Abundance data were not obtained for block D.

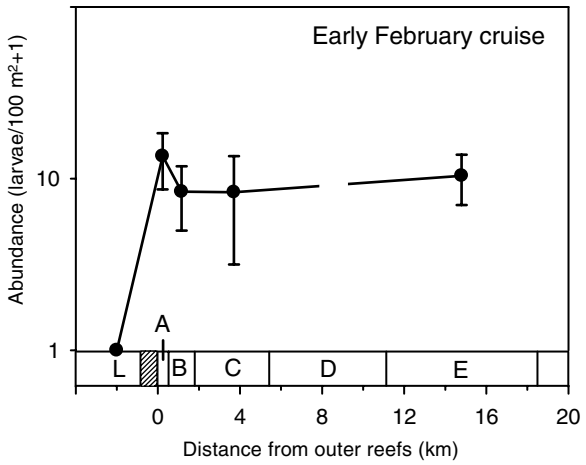

Figure 4

Mean abundance (larvae/100 m^2+1 [± standard error]) of *Thunnus albacares* (yellowfin tuna) larvae with distance from the outer reefs of the Great Barrier Reef during the early February cruise in the Coral Sea. Data points indicate the midpoint of sampling blocks (A–E) by distance, except for the Great Barrier Reef Lagoon (L on the *x* axis) the display of which is categorical and does not reflect the true distance from the other blocks. The *y* axis is $\log_{10}$ scale. The *x* axis shows the width of each sampling block (km). The hatched area on the *x*-axis indicates the position of the outer reef area of the Great Barrier Reef. No significant differences were found among blocks (ANOVA, P=0.06). Abundance data were not obtained for block D.

(K-S test, P<0.01, Fig. 7A) and late February (K-S test, P<0.02, Fig. 7B) cruises. A similar pattern was found for the late November cruise, with the result approaching significance (K-S test, 0.05<P<0.10, Fig. 7C). Despite a greater proportion of smaller larvae present in the inshore zone, small (~2 mm SL) *K. pelamis* larvae were present in the offshore zone on all cruises. There was also a greater proportion of small (3–4 mm SL) *T. albacares* larvae in the inshore zone, compared with the offshore zone, on the early February cruise (K-S test, P<0.02, Fig. 8). Not enough *T. albacares* larvae were caught in each zone on other cruises for statistical analysis; however examination of size-frequency data indicated that there may also have been a greater proportion of smaller *T. albacares* larvae in the inshore zone on the late November cruise. No significant differences in size-frequency distributions were found for *T. alalunga* larvae between the inshore and offshore zones on either the early November (K-S test, P>0.2, Fig. 9A) or late November (K-S test, P>0.2, Fig. 9B) cruises. There was also no significant difference in the size of *Auxis-Euthynnus* larvae between the inshore and offshore zones on the early February cruise (K-S Test, P>0.2, Fig. 9C).

Discussion

Mean near-reef (<4 km offshore) abundances of tuna larvae in the Coral Sea (range 20–120 larvae/100 m^2) were similar to those found around the Hawaiian island of Oahu (~3–80 larvae/100 m^2, Boehlert and Mundy, 1994) and similar to estimates of near-reef abundance from French Polynesia (45–75 larvae/100 m^2, Leis et al., 1991). Although these values were not much greater

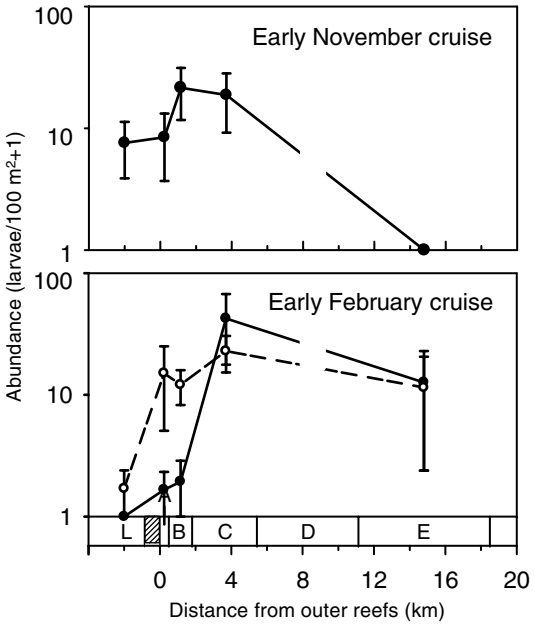

Figure 5

Mean abundance (larvae/100 m^2+1 [± standard error]) of larvae with distance from the outer reefs of the Great Barrier Reef for *Euthynnus affinis* (kawakawa, full line) larvae during the early November and early February cruises, and for *Auxis-Euthynnus* (dashed line) larvae during the early February cruise, in the Coral Sea. Data points indicate the midpoint of sampling blocks (A–E) by distance, except for the Great Barrier Reef Lagoon the display of which (L on the *x* axis) is categorical and does not reflect the true distance from the other blocks. The *y* axis is $\log_{10}$ scale. The *x* axis shows the width of each sampling block (km). The hatched area on the *x* axis indicates the position of the outer reef area of the Great Barrier Reef. No significant differences were found among blocks on either the early November (ANOVA, P=0.14) or early February (ANOVA, P=0.11) cruises for *E. affinis* larvae, or on the early February cruise (ANOVA, P=0.06) for *Auxis-Euthynnus* larvae. *Auxis-Euthynnus* larvae were not sufficiently abundant on the first cruise for statistical analysis. Abundance data were not obtained for block D.

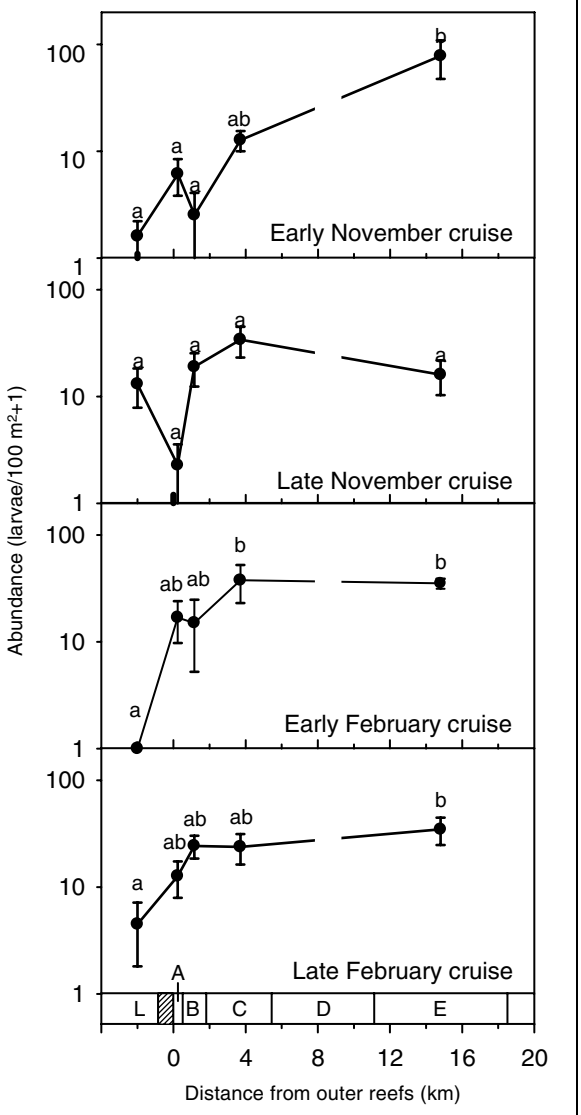

Figure 6

Mean abundance (larvae/100 m^2+1 [± standard error]) of *Katsuwonus pelamis* (skipjack tuna) larvae with distance from the outer reefs of the Great Barrier Reef during four cruises in the Coral Sea. Data points indicate the midpoint of sampling blocks (A–E) by distance, except for the Great Barrier Reef Lagoon the display of which (L on the *x* axis) is categorical and does not reflect the true distance from the other blocks. The *y* axis is $\log_{10}$ scale. The *x* axis shows the width of each sampling block (km). The hatched area on the *x* axis indicates the position of the outer reef area of the Great Barrier Reef. Within a cruise, if data points share a lowercase letter, they were not significantly different from each other according to Tukey's *post hoc* test. Abundance data were not obtained for block D.

than those determined for oceanic sites elsewhere (24–80 larvae/100 m^2, Strasburg, 1960; Nakamura and Matsumoto, 1966), the larvae of most tuna species were more abundant within 5.6 km of the Great Barrier Reef than further offshore in the Coral Sea. This pattern was consistent among cruises for particular taxa, indicating that near-reef larval distributions persist over seasonal time scales.

Larvae of the genus *Thunnus* may generally be more abundant in near-reef waters than farther offshore, because in all studies of tuna larvae in near-reef waters consistently high concentrations or abundances of *Thunnus* larvae have been found there. Greatest abundances of *Thunnus* larvae were often found within 2 km of the outer Great Barrier Reef in the present study,

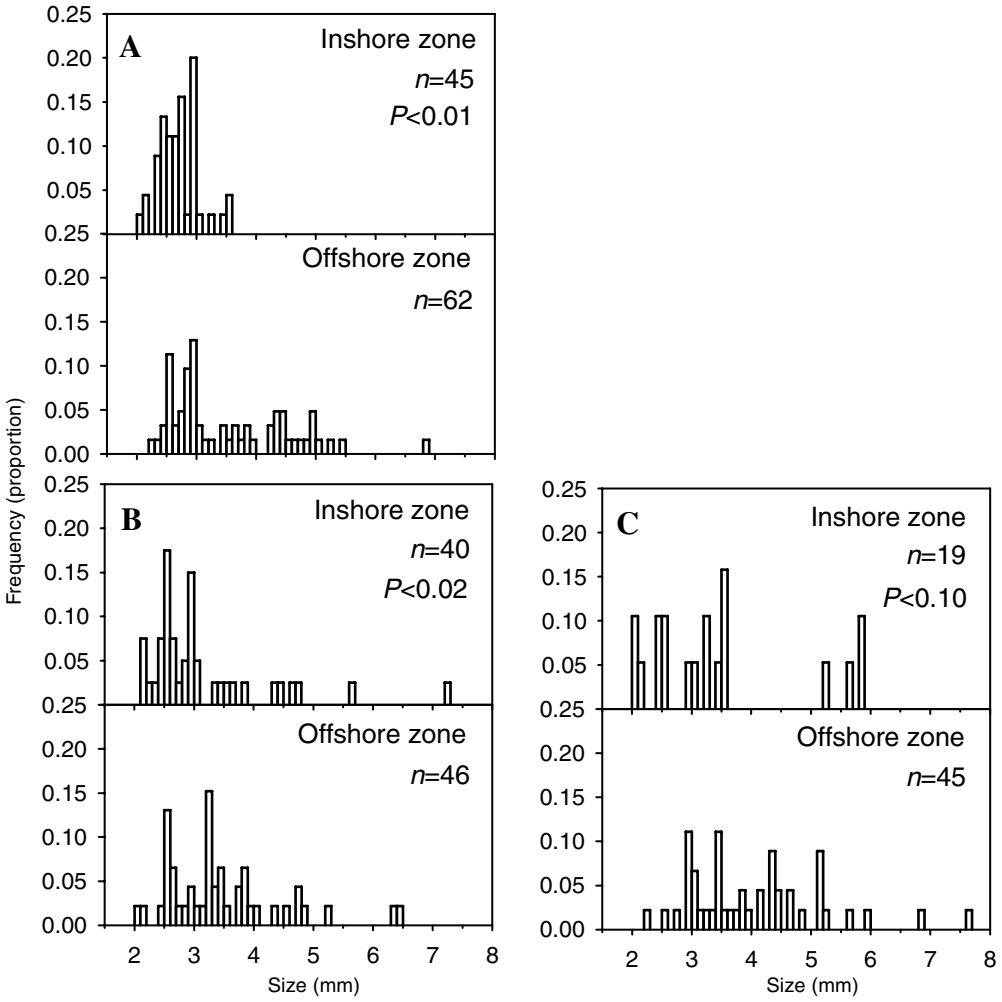

Figure 7

Size-frequency distributions for *Katsuwonus pelamis* (skipjack tuna) larvae from inshore and offshore zones during the (**A**) early February, (**B**) late February, and (**C**) late November cruises in the Coral Sea. Standard length (mm) of larvae was measured to the nearest 0.1 mm. *P*-values refer to the significance of Kolmogorov-Smirnov (K-S) tests conducted between the inshore and offshore zones within a cruise.

and, as with our findings, small (≤3.0 mm SL) *Thunnus* spp. larvae were ~10 times more abundant 1.8 km offshore, than 9.3 km offshore, of the leeward side of Oahu Island (Boehlert and Mundy, 1994). In an earlier study at Oahu Island high concentrations (up to 220 larvae/500 m^3) of *T. albacares* larvae were found within 2 km of shore (Miller, 1979), and similar concentrations (up to 224 larvae/500 m^3) of *Thunnus* spp. larvae (either *T. albacares* or *T. alalunga*) were found in samples taken within 200 m of reefs in French Polynesia (Leis et al., 1991). The present study is the first to investigate near-reef distributions of tuna larvae outside of central Pacific Ocean island environments and thus extends the near-reef distributional pattern to include continental slope environments of the western Pacific Ocean, but further research on on-offshore patterns of abundance in other regions is required to confirm the generality of this phenomenon.

Considerable differences in on-offshore larval distributions may exist among genera of tuna, perhaps even among species, and these differences may not necessarily reflect similarities in adult distributions. We have confirmed the opposing on-offshore distributions of *Thunnus* spp. and *K. pelamis* larvae previously discovered in Hawaii, where *Thunnus* spp. larvae were more abundant near the reef on the leeward side of Oahu Island, while *K. pelamis* larvae increased in abundance in the offshore direction (Boehlert and Mundy, 1994). Interestingly, the on-offshore distributions of *Thunnus* spp. larvae in the Coral Sea were more similar to the larval distributions of *E. affinis* (and possibly *Auxis* spp.) than to the distributions of *K. pelamis* larvae.

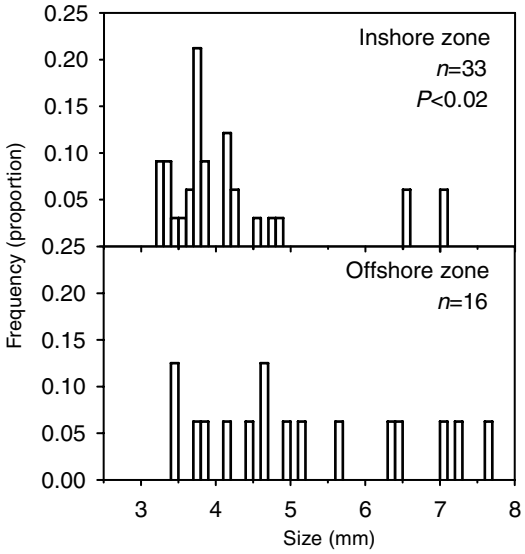

Figure 8

Size-frequency distributions for *Thunnus albacares* (yellowfin tuna) larvae from inshore and offshore zones during the early February cruise in the Coral Sea. Standard length (mm) of larvae was measured to the nearest 0.1 mm. The *P*-value refers to the significance of a Kolmogorov-Smirnov (K-S) test conducted between the inshore and offshore zones.

This finding is remarkable, considering *T. albacares* and *K. pelamis* are considered to be truly oceanic species with similar adult distributions, whereas adult *E. affinis* and *Auxis* spp. have coastal distributions (Collette and Nauen, 1983). Because of potential distributional differences, further research on the near-reef larval distributions of other tuna species is required; however this may be difficult considering the relative rarity of the larvae of some species (e.g., *T. tonggol*).

The greater abundances of small *Thunnus* spp. and *Auxis-Euthynnus* larvae within 5.6 km of the outer Great Barrier Reef indicates that these species may have spawned more intensely or more frequently (or both) in this area, than farther offshore, during the study period. Larvae of *Thunnus* spp. were all <3.2 mm SL because of the limits of our ability to identify small larvae, and therefore their near-reef distribution observed on at least three cruises was most likely the result of near-reef spawning activity of *T. albacares* (which likely comprised most of the *Thunnus* spp. larvae). In support of this conclusion, there was a greater proportion of small *T. albacares* larvae within 1.85 km of the outer Great Barrier Reef than farther offshore during the early February cruise. *Auxis* spp. or *E. affinis* (or both) may have also spawned near the reef in early February, as indicated by the greater abundance of small (<2.3 mm SL) *Auxis-Euthynnus* larvae within 5.6 km of the outer GBR, which approached significance (ANOVA, $P=0.06$, Fig. 5). Their narrow size range (1.9–2.2 mm SL) did not, however, allow for a comparison of sizes between inshore and offshore zones. Although it is likely that initial spawning distributions of the larvae of these two taxa would have been modified to some degree by subsequent physical or biological processes, or both (see below), their small size (and likely young age) would have minimized the time between spawning and capture and therefore would have reduced the potential effect of subsequent modification on their observed distributions.

The greater abundance and size of *K. pelamis* larvae offshore indicates that observed distributions of this species most likely arose from considerable modification of initial spawning distributions. Like *T. albacares*, *K. pelamis* likely spawned more intensely or more frequently, or both, within 1.85 km of the outer Great Barrier Reef during the study period because there was a greater proportion of small larvae within the inshore zone than in the offshore zone, on two, possibly three, cruises. Larval abundance of this species increased with increasing distance from the outer Great Barrier Reef, however, indicating that larvae may have accumulated in the offshore area. A similar pattern of increasing abundance offshore, combined with smaller larvae near the reef, was found for *K. pelamis* on the leeward side of Oahu Island, Hawaii (Boehlert and Mundy, 1994); however no mechanism was suggested to account for these patterns. Differential growth or mortality, or both, for *K. pelamis* larvae may have occurred between near-reef and offshore areas; however we believe that offshore transport by means of physical mechanisms (see below) provides the best explanation of observed distributions, at least in the Coral Sea.

The scarcity of larvae of any tuna taxon in the Great Barrier Reef Lagoon, even when offshore abundances were quite high, indicates that little, if any, spawning occurred there. The moderate abundances of *K. pelamis* (13.1 larvae/100 m^2) and *T. alalunga* (10.3 larvae/100 m^2) larvae in the lagoon on the late November cruise were most likely caused by advection of larvae through the inter-reef passages from spawning locations on the seaward side of the outer reefs, either by onshore winds, or by tidal movement (Leis et al., 1987). We cannot exclude the possibility that some individuals of these species spawned inside the lagoon during the study period, but such spawning would have represented only a small proportion of total spawning effort.

The high abundances of *Thunnus* spp. and *T. alalunga* larvae found near the reef in the present study likely resulted, at least in part, from onshore advection due to wind-driven currents interacting with the surface-orientated distribution of the larvae. The relatively consistent light to moderate onshore (E-SE) winds during the study period in the Coral Sea most likely resulted in shoreward advection of surface water layers. Onshore advection of surface water and subsequent downwelling on the windward side of the outer reefs, combined with a shallow vertical distribution of larvae, was suggested as a possible mechanism resulting in

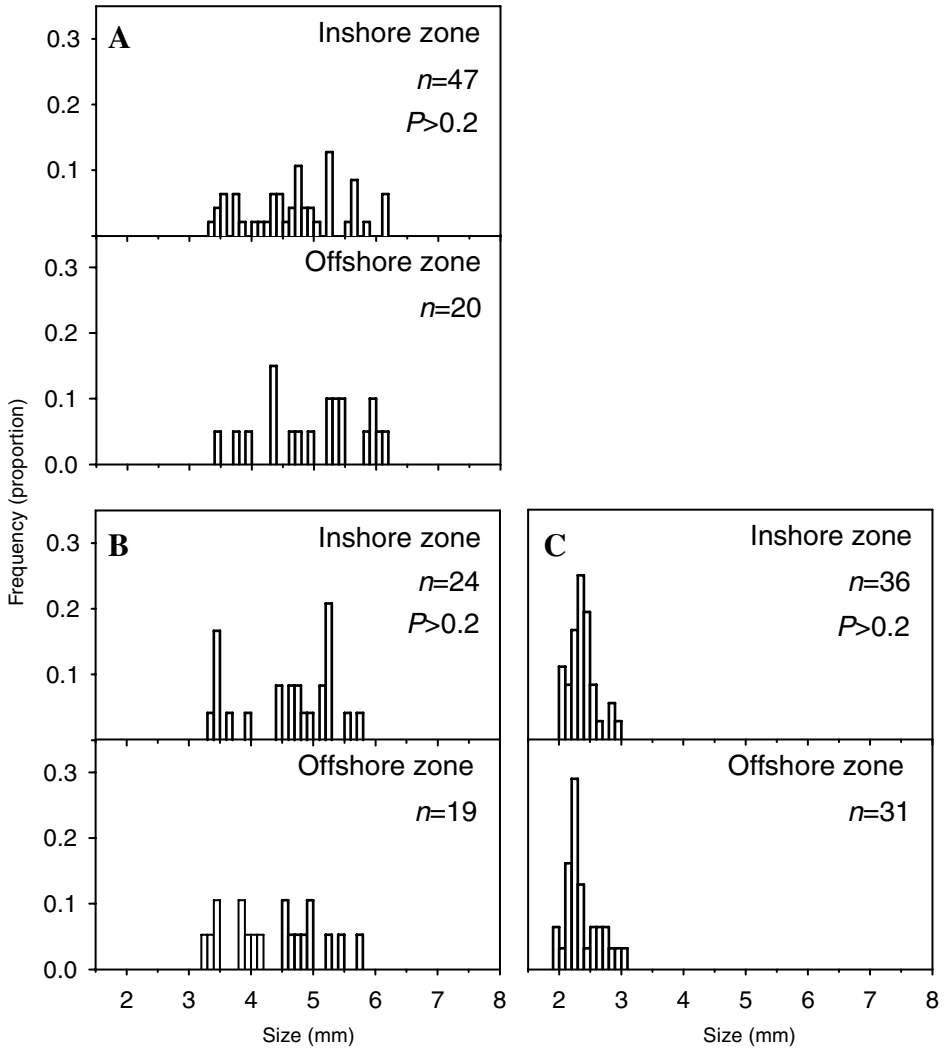

Figure 9

Size-frequency distributions for larvae from inshore and offshore zones of the Coral Sea of *Thunnus alalunga* (albacore) during the (**A**) early November, and (**B**) late November cruises, and for *Auxis-Euthynnus* during the (**C**) early February cruise. Standard length (mm) of larvae was measured to the nearest 0.1 mm. *P*-values refer to the significance of Kolmogorov-Smirnov (K-S) tests conducted between the inshore and offshore zones within a cruise.

near-reef (within 2 km offshore) distributions of *Makaira indica* (black marlin), *M. mazara* (blue marlin), and *Istiophorus platypterus* (Indo-Pacific sailfish) larvae in the Coral Sea ("the anstau hypothesis," Leis et al., 1987). The istiophorid larvae examined by Leis et al. (1987) for horizontal distributions were taken from the same samples used in this study. Like billfish, larvae of *Thunnus* spp. also have relatively shallow distributions; greatest abundances were found in the upper 20 m of the water column around Oahu Island (Boehlert and Mundy, 1994) and higher concentrations were found at 5 m depth than at 10 m depth in French Polynesia (Leis et al., 1991). Larvae of *T. atlanticus* (blackfin tuna) were caught in greatest numbers in the upper 20 m of the water column in the northern Caribbean Sea, and few larvae were caught below 40 m depth (Hare et al., 2001). We cannot confirm this hypothesis, however, because we did not take direct measurements of either currents or the vertical distributions of tuna larvae during the present study period.

Downwelling on the seaward side of the outer reefs in the Coral Sea could account for the simultaneous occurrence of opposing on-offshore distributions of *K. pelamis* and *Thunnus* larvae because of known differences in the vertical distributions of larvae between these two genera. Larvae of *K. pelamis* have deeper distributions

than *Thunnus* spp. larvae (Boehlert and Mundy, 1994; Hare et al., 2001), and migrate into deeper water during the day, at which time larvae of *Thunnus* spp. move into surface layers (Richards and Simmons, 1971; Davis et al., 1990b). It is therefore possible that while *Thunnus* spp. and *T. alalunga* larvae in the present study were advected shoreward by wind-driven surface currents, and accumulated there by a tendency to remain near the surface, larvae of *K. pelamis* were advected offshore by deeper return flow originating from downwelling near the outer reefs. At the least, *K. pelamis* larvae would not accumulate near the reef front because they would not be expected to counter the putative downwelling at those locations.

The larger size and greater abundance of *K. pelamis* larvae offshore indicate that the larvae of this species likely accumulated there, providing support for the hypothesis of offshore physical transport at depth for this species. And although *T. albacares* and *T. alalunga* larvae were not larger inshore, as would be expected if larvae were transported onshore and accumulated near the reef, larvae of these species >3.5 mm SL were common near the reef, which was not the case for *K. pelamis*. It is possible that the size distributions of *T. albacares* and *T. alalunga* larvae in the Coral Sea may have been affected by greater mortality of larger size classes in the inshore zone than in the more offshore waters. It has been hypothesized that predation rates of larval fish are higher in near-reef waters than in the open ocean (Johannes, 1978), and direct observations of late-stage reef fish larvae have shown that larvae near reefs feed less and are preyed upon more often than larvae farther offshore (Leis and Carson-Ewart, 1998).

The patterns of on-offshore distribution of tuna larvae documented here support the hypothesis that at least some tuna species have high larval abundances near reefs in the Tropical Pacific Ocean. We conclude that fine-scale (1–10 km) on-offshore distributions of tuna larvae found in the Coral Sea were most likely the result of relatively near-reef spawning patterns of adults (<10 km offshore) subsequently modified by wind-driven onshore currents and presumed downwelling in front of the outer reefs of the Great Barrier Reef. To account for different horizontal distributions of larvae among taxa, we suggest that putative opposing flow directions between the surface layers and deeper water may have interacted with the taxa-specific vertical distributions of larvae. An investigation of physical and biological factors, vertical distributions of larvae, and the abundance and distribution of spawning adults near reefs is required to further our understanding of the primary causes of on-offshore distributions of tuna larvae.

Regardless of how distributions occurred, near-reef areas may generally be more important than offshore areas for the production of *T. albacares* and *T. alalunga* larvae, and possibly other large pelagic species. It is now evident from four studies that larvae of *T. albacares* and *T. alalunga* are abundant in near-reef (<5 km offshore) waters, and in the two studies where larval tuna abundances near a reef were compared with larval tuna abundance in offshore areas, higher abundances of *Thunnus* spp. larvae were found near the reef (the present study; Boehlert and Mundy, 1994). These studies also indicate that *K. pelamis* may, at least, spawn close to shore, although their larvae are not most abundant there. Larvae of other large pelagics, such as billfishes, may also be generally more abundant near reefs, as indicated by the near-reef abundance of larvae of three species in our study area (Leis et al., 1987). Near-reef areas have not received much attention in studies of distribution and abundance of larvae of large pelagic predators like tunas and billfishes. If the patterns found thus far are a general occurrence in tropical regions, larval abundance surveys that do not include these areas may underestimate true abundances. It must be kept in mind, however, that near-reef areas are much smaller than oceanic areas. Therefore, in spite of higher abundances (per unit of area) of larvae near reefs, the offshore areas may provide the bulk of the recruits to adult populations, because of the vast areas involved. As yet, there are no data on the survival rates of larvae near reefs compared to the survival rates of larvae offshore, or on their relative contributions to spawning populations.

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