

Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters

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Abstract—A study of ocean current patterns with associated biological measurements was conducted to ascertain if ocean eddies can transport and retain the planktonic larvae of coastal marine animals near islands for sufficient duration to complete the pelagic developmental phase. Our results indicate that (1) the mesoscale eddy/current systems can entrain and entrap larvae from the reefs, (2) sufficient residence time exists for many reef fish species to complete their pelagic development phase, and that (3) passive drift of larvae back to reefs is possible, although self-motile mechanisms may be more important.

INTRODUCTION

IN RECENT years a new phenomenological picture of the kinematics and structure of ocean currents has emerged due to new sampling schemes, instruments and concepts. Energetic time and space variability is now well known to take the form of eddies, jets, fronts, rings, filaments, etc. (ROBINSON, 1983). The transport processes implied by this new picture of the physical fields are very different from those previously conceived (HAIDVOGEL *et al.*, 1983) and these newly recognized transport processes should affect biological processes (e.g. ANGEL and FASHAM, 1983; LEGENDRE and DEMERS, 1984). Investigations have been undertaken to explore these processes in a variety of circumstances, and in particular eddies have been implicated to have profound effects on the distribution of pelagic marine organisms. For example, eddies can entrain planktonic animals and advect them horizontally (e.g. THE RING GROUP, 1981). To date a few studies have considered how open ocean currents and eddies may impact coastal marine animals, especially those with a planktonic larval phase (e.g. BODEN, 1952; EMERY, 1972; JOHANNES, 1978; LOBEL, 1978; LEIS, 1982a,b; LEIS and GOLDMAN, 1983; WROBLEWSKI and CHENEY, 1984; FLIERL and WROBLEWSKI, 1985). We report here results from a study carried out on the effect of eddy currents on the life-cycle of Hawaiian reef fishes. The overall goal of our research is aimed at the construction of a conceptual model of the variability and scale of ocean currents which impact the population biology of coastal marine species (LOBEL and ROBINSON, 1983).

Eddies and larval fish transport mechanisms can result in fluctuations in recruitment with implications for fisheries (LASKER and SHERMAN, 1981; McFARLAND, 1982; RICHARDS, 1982) and reef fishes community ecology (SALE, 1978, 1980a; HELFMAN, 1978;

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SMITH, 1978; ANDERSON *et al.*, 1981; BARLOW, 1981). Such larval transport can affect evolution and maintenance of endemic island species, especially fishes in Hawaii (LOBEL, 1978; LOBEL and ROBINSON, 1983); also such processes can determine offshore concentrations of plankton, the mechanisms for their formation, and their relationship to the distribution of pelagic gamefishes.

Comprehensive sampling of zooplankton in Hawaiian waters began with KING and HIDA (1954). They concluded "that although the abundance of zooplankton was remarkably uniform throughout island waters, there were certain areas which were consistently richer or poorer than other areas." Areas of highest zooplankton concentrations (shown in their Fig. 10) were later found to be general locations at which mesoscale eddies were

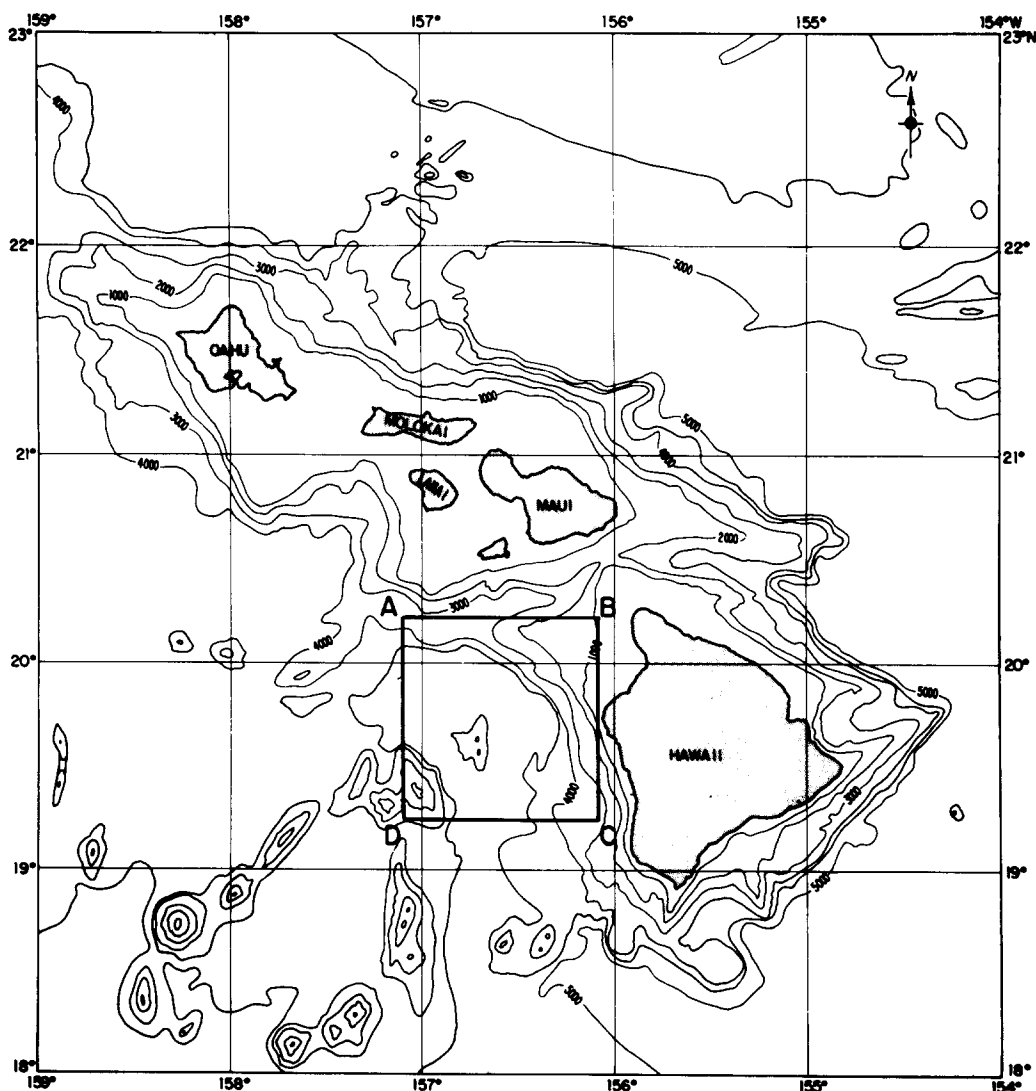


Fig. 1. The domain of this study is delineated and referenced by points A, B, C, and D and corresponds so in all subsequent geographic figures. Bathymetry is contoured in 500 m intervals. Chart is modified from WILDE *et al.* (1980).

observed, especially off the island of Hawaii (PATZERT, 1969). These data, albeit suggestive rather than definitive, presented intriguing possibilities which were left unexplored for many years.

Research specifically on larval fishes in Hawaii was initiated by J. Miller and co-workers (MILLER, 1973, 1979; MILLER *et al.*, 1979; LEIS, 1982a,b; LEIS and MILLER, 1976; WATSON and LEIS, 1974). Earlier, SALE (1970) briefly described the offshore distribution of acanthurid larvae entrapped in an eddy off the island of Oahu. He reported that these acanthurid larvae were restricted to the upper 100 m and that the largest catch came from "the northeast edge of a large gyral southwest of Oahu." This eddy had a rotation period of 5 to 6 days and was located about 25–50 km from shore. Subsequent studies by Miller, Leis and Watson were conducted nearshore; maximum distances from shore sampled in their studies were 5 km (MILLER, 1973; MILLER *et al.*, 1979); 2 km (MILLER, 1979); 3 km (LEIS, 1982a,b); 12 km (LEIS and MILLER, 1976); Kaneohe Bay, Oahu (WATSON and LEIS, 1974). On the basis of these nearshore samples and without the benefit of accompanying physical oceanographic details, LEIS (1982b) concluded that ocean eddies probably do not function as a mechanism for larval retention in Hawaiian waters.

In this paper, we examine how an eddy can transport and entrain passive drifting material near islands, and how such passive tracers can be swept on and off the reef by transient mesoscale currents. From a detailed composite data set we illustrate what may happen to eggs and larvae spawned by coastal marine fishes at a time when a cyclonic eddy is the dominant mesoscale current offshore an island.

The results were obtained in the period from July to September 1982. The flow was determined by measurements of temperature and near-surface velocity. Shore-tracked drifters launched nearshore from a Boston whaler and satellite infrared imagery identified a cyclonic eddy with swirl speeds up to 3 kn northeast of Keahole point from mid-July to mid-September. In early September the eddy began to move southward. XBT surveys were conducted 21–23 July and 10–12 September. Biological samples were obtained 23–26 July. We found and observed: (a) a geostrophic mesoscale cyclonic eddy off the lee of the island of Hawaii (Kona coast) that we observed to remain in the area for about 2 months, (b) the entrainment of drifting drogues from initial locations over reefs and adjacent offshore waters into the eddy, (c) the subsequent transport of entrained drogues back to nearshore locations, (d) the distribution of larval fishes and zooplankton biomass across the cyclonic eddy field, with fish larvae most numerous in the main swirl near the frontal zone.

PHYSICAL MEASUREMENTS

The patterns of ocean currents were defined by the trajectories of near-surface drogues (radio-tracked Lagrangian drifters), by the temperature field measured with expendable bathythermographs (XBTs) and by the interpretation of features on satellite infrared photographs of sea surface temperatures. The study domain is delineated in Fig. 1 by points ABCD and is so referenced in other figures.

Velocity measurements

Current drogues used as Lagrangian tracers of the surface currents, were deployed nearshore and over reefs. Drogues were also deployed in offshore waters to delineate the

structure of the mesoscale currents. These drogues were set to a water depth of 4 m, windage was minimal (LOBEL and ROBINSON, 1985).

Drogue positions were determined by radio-telemetry by acquiring a time series of measurements from coastal positions. The range of signal reception was approximately 81 km with bearing fixes of about 1° accuracy. The size of the area plotted for drogue positions ranged from 1 km^2 or less when nearshore to 40 km^2 at distances beyond 55 km. Several figures show the last position of a drogue in the center of tracking range. In these cases, transmitter or drogue failure most likely accounts for their disappearance

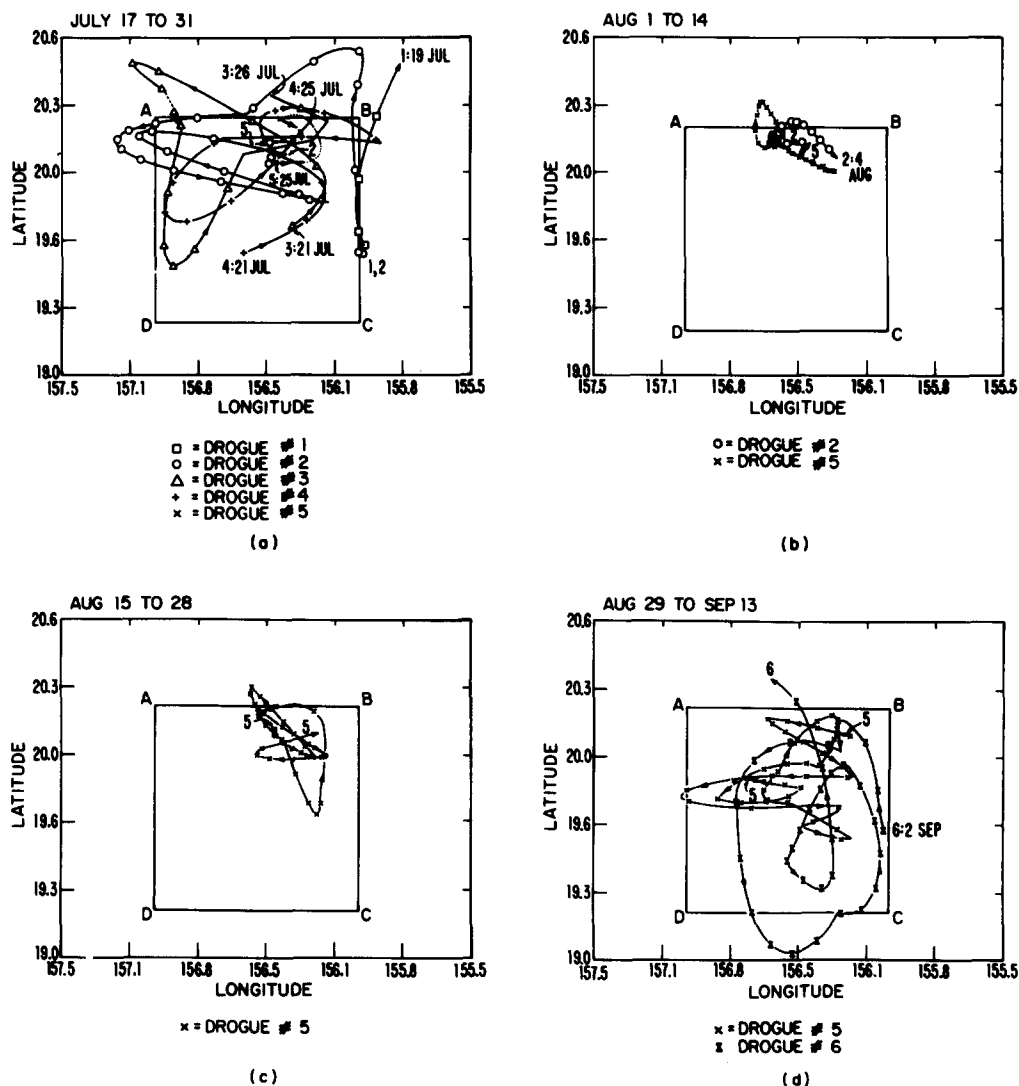


Fig. 2. Composite drogue trajectories for biweekly periods from 17 July to 13 September 1982. Each drogue is denoted by a symbol spaced at 8 h intervals interpolated along a smoothed drift trajectory. The direction of flow is shown by arrowheads. Refer to Fig. 1 for location. (a) Trajectories of 5 drogues, 17–23 July. (b) Trajectories of 2 drogues, 1–14 August. (c) Trajectory of 1 drogue, 15–28 August. (d) Trajectories of 2 drogues, 29 August–13 September.

rather than the drogues having been rapidly advected away. Eight drogues were deployed in the period 17 July–13 September 1982. Their trajectories are shown in snapshots of 2 weeks duration in Fig. 2.

For 2 months prior to mid-July, several additional drogues were deployed and tracked in the same area: 9–12 May, 6–12 June, 17 June–7 July, and 22 June–15 July. All drogues were tracked until signal reception ceased. Surveillance for drogues signals was maintained at regular intervals afterwards but none of these earlier drogues returned after 15 July. The trajectories of these drogues and corroborating evidence of infrared satellite photographs and current meter records suggest that the cyclonic eddy described below did not develop until mid-July.

Two drogues were deployed on 17 July and they drifted northward. One drogue (No. 1) was carried near Upolu Pt. and into the Alenuihaha Channel; its signal vanished on 19 July (Fig. 2a). The other drogue (No. 2) drifted farther offshore and was entrained by the cyclonic eddy. This drogue remained in local waters for 17.5 days. Its disappearance was most probably due to transmitter power/mechanical failure, based on the trajectories of other drogues also in the water at the same time. These two drogues plus three others described below are shown in Fig. 2a.

We deployed four drogues offshore on 21 July to see if they would be transported to the same region as the drogues released nearshore on 17 July (Fig. 2a). The positions of two of these four drogues (Nos 3 and 4) are shown in Fig. 2b. The biological question was “would ichthyoplankton already adrift offshore become entrained by the eddy?” These drogues were equipped with a special transmitter for relaying sea surface temperature data. Unfortunately, this option did not provide useful data, consumed power making the transmitters short-lived (about 36 h). All four drogues moved northward and appeared to be influenced by the eddy. The two drogues closest to shore moved off together but stopped transmitting in less than a day. One drogue appeared to be entrained well within the eddy, looping tightly through about one and a quarter cycles during its 5 day lifetime. We were only able to fix the drogue launched farthest from shore at infrequent intervals. It approached very close to shore before becoming entrained well within the eddy as was its nearest neighbor and lasted 4 days.

A single drogue was deployed in the cyclonic eddy's central area as determined by XBT data on 25 July (No. 5 in Fig. 2a). The drogue was tracked for 49.25 days before signal reception ceased. It drifted within the same general vicinity until 1 September, after which it moved to the south. Bathythermograph data obtained at the time of deployment and also later (19 August) show that it remained in the eddy's core.

The radical departure of drogue No. 5 (Fig. 2d) from its previous positions (25 July – 1 September, Figs 2b and c) led us to deploy drogue No. 6 on 2 September (Fig. 2d). This drogue was also entrained by the cyclonic eddy. Its trajectory appeared to circumnavigate the eddy in wide loops, finally being swept out of range to the northwest after 2 weeks and three loops (Fig. 2d).

Figure 2a clearly illustrates the entrapment into the eddy of drogues originating offshore and at the reef-edge, as well as the thermocline mesoscale jet flowing to the northeast apparent in Figs 3 and 6 (below). It also shows that tracer material circulating in the periphery may be carried back to the reef-edge. Figures 2b and c provide definitive evidence of the power of the eddy to retain entrapped drifting material. Figure 2d depicts the southward movement of the feature which was accompanied by the ejection of tracer material from dead center into the outer swirl of the broadening feature. The speeds

Table 1. Drifter statistics

Drogue	Number of segments	Average speed (cm s ⁻¹)	Maximum speed (cm s ⁻¹)	Minimum speed (cm s ⁻¹)	S.D. (cm s ⁻¹)
1	3	65	114	16	47
2	11	36	155	11	37
3	8	41	271	13	53
4	39	22	164	1	24
6	12	59	129	21	29

$$* \text{ S.D.} = \frac{\Sigma(\mu - \bar{\mu})^2 t^{1/2}}{T},$$

where t = number of hours between observations. T = total number of hours.
 μ = speed between fixes and $\bar{\mu}$ = mean speed.

during these periods are shown in Table 1. The maximum speed of drogue No. 3 we believe to be real at 2.7 m s⁻¹. It is the highest value observed to date. Maxima of about 1.5 m s⁻¹ were common. The set and drift of our research vessel was consistent with these measurements of Table 1.

Temperature measurements and geostrophic flow

Expendable bathythermographs were deployed from a fast-moving boat to map the temperature distributions. The Sippican Mk2 Recorder and T-4 XBT probes were used for the measurements. By using known T-S relationships for the region (SCRIPPS INSTITUTION OF OCEANOGRAPHY, 1963a,b, 1965), density can be inferred and the flow of geostrophic mesoscale currents calculated.

Two XBT mapping surveys were conducted with station spacing between 7 and 10 km along the cruise track (Fig. 3). The first survey took place from 21 to 23 July after the drogues had indicated the existence of the eddy. Additional XBT's were deployed 23–26 July and a few measurements were made on 19 August with a mechanical BT (intercalibrated with XBTs). From 10 to 12 September as the eddy began to move, the second survey was carried out to define how far and in what direction the eddy had moved and to investigate structural changes.

The positions and size of the eddy is shown by NOAA-7 satellite infrared photographs of sea surface temperatures. A mass of cold water in the location of the cyclonic eddy on 31 July is clearly shown in Fig. 4a. Figure 4b shows the cyclonic eddy on 8 September and Fig. 4c shows the eddy farther offshore on 17 September.

Results are presented as contour maps of the 24 and 20°C isotherm depth in Fig. 3 and of dynamic height in Fig. 5. Contour maps were constructed using the statistical techniques and standard programs of the Harvard Physical Oceanography group (CARTER, 1983; ROBINSON and LESLIE, 1985; CARTER and ROBINSON, 1985).

The parameters used for the statistical objective analysis of isotherms were as follows: number of influential points, 7, and influential distance, 55 km. The parameters used for the dynamic height analysis were: number of influential points, 4; influential time, 20 days, and influential distance, 20 km. The exponential correlation function has an e-folding distance of 55 km and folding time of 30 days.

The isotherms in July (Fig. 3a) clearly show a mesoscale cyclonic eddy feature with a radius of about 25–30 km located about 55 km northwest of Keahole Pt., Hawaii. The near-surface structure also indicates that the southwest edge of the eddy coincides with

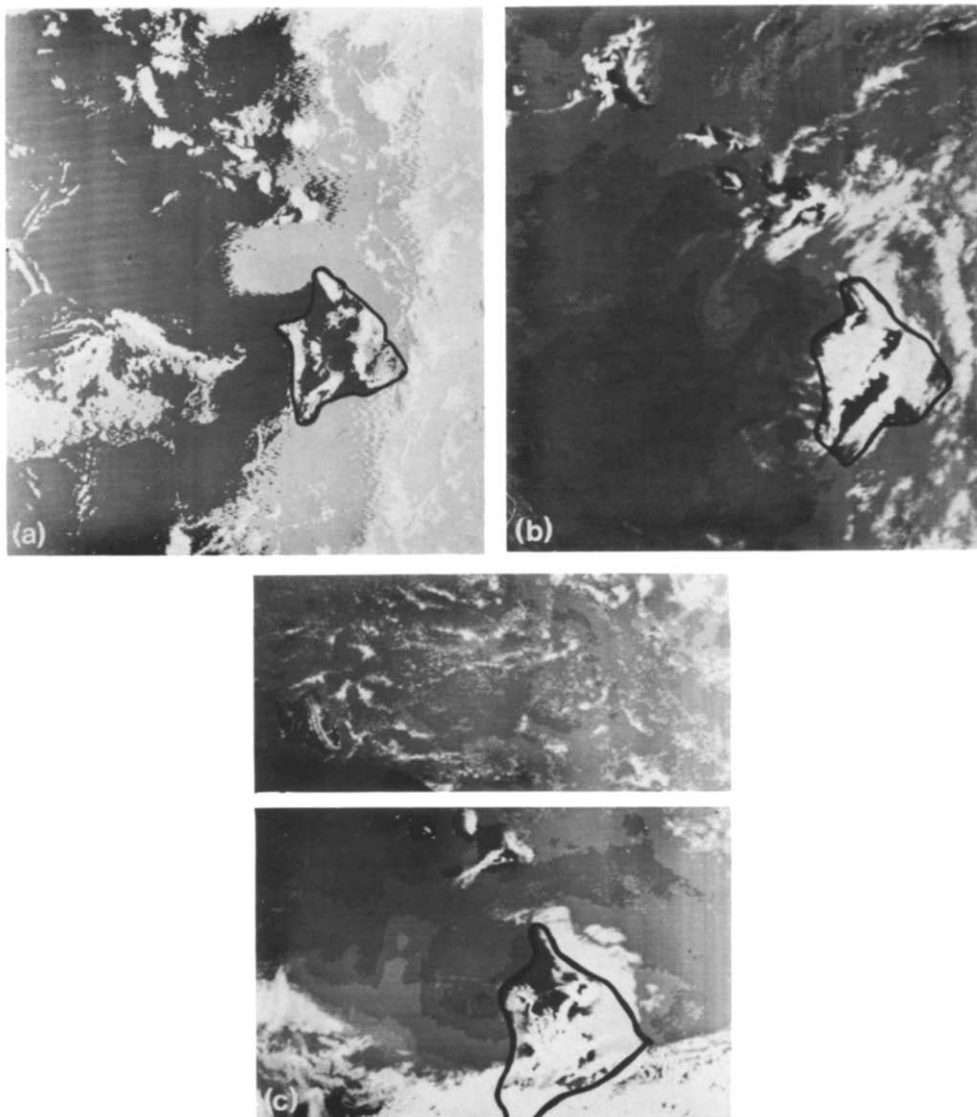


Fig. 4. Infrared photographs of sea surface temperatures obtained by the NOAA-7 satellite and processed Det. 4, 1st Weather Wing, USAF, Hickam Air Force Base, Honolulu. The photographs display shades of grey with the lighter shades representing cooler temperatures. The bright white areas depict clouds obscuring the sea surface. The island of Hawaii is outlined. (a) Photo from 30 July 1982. There are four shades of grey on the picture; the lighter the shade, the cooler the temperature. The Island of Hawaii is outlined. The circular cold-water mass extending from the Alenuihaha Channel between Hawaii and Maui covers the region of the cyclonic eddy defined by XBT measurements (Fig. 3a). (b) IR Photo taken on 7 September 1982 shows a swirl of cold water rotating counter-clockwise off the west coast of Hawaii in the vicinity of the cyclonic eddy defined by XBT measurements (Fig. 3b). (c) Photo from 16 July 1982, 3 days after the eddy moved west, carrying the drogues in it beyond tracking range. A cold-core feature is indicated far west of Hawaii and south of Lanai.

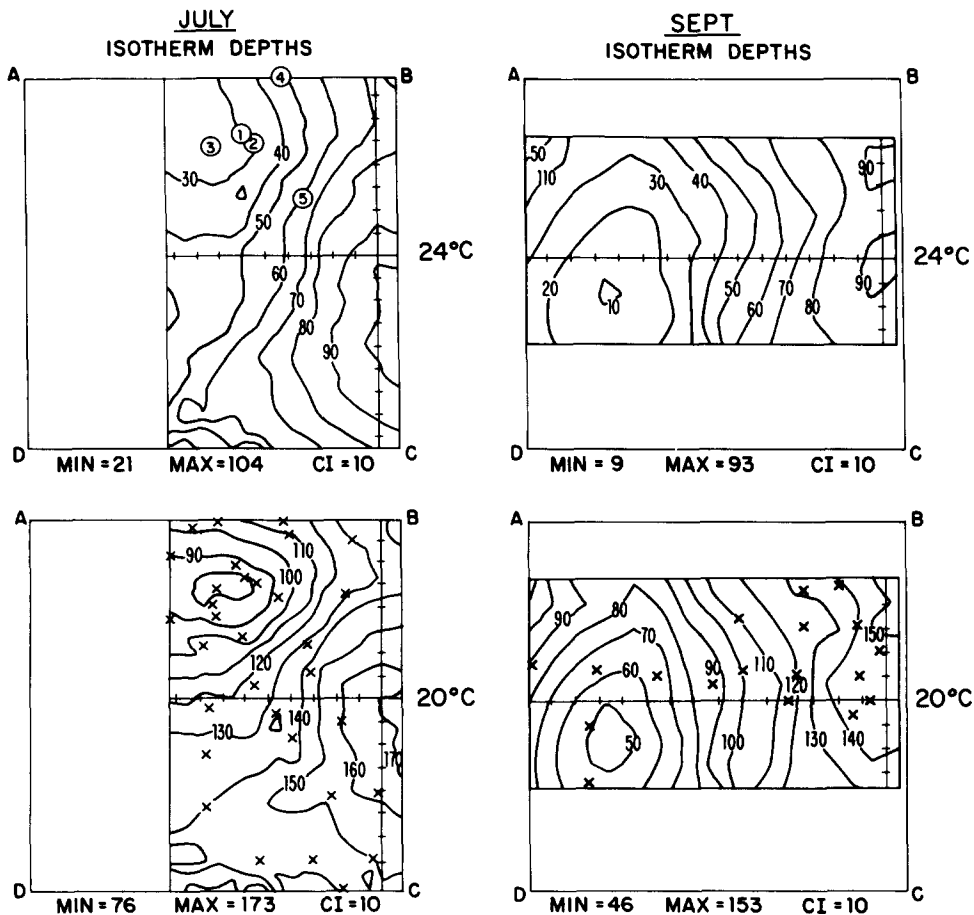


Fig. 3. The cyclonic eddy defined by the patterns of the 24 and 20°C isotherms in (A) July and (B) September. Isotherm depth is given in meters with a 10 m contour interval (CI). The minimum (min) and maximum (max) isotherm depths are given for each plot. The July 24°C isotherm plot also denotes positions of the plankton sample stations (1–5), see Table 1. The 20°C plot shows each XBT station (x). The tick-marked axes have an origin that corresponds geographically with Keahole Pt., Hawaii (19.73°N, 156.07°W). Tick-mark interval is 6 km in A and 7 km in B. The domain delineated by points A, B, C, D is shown in Fig. 1.

an elongated jet flowing to the northeast. The September data (Fig. 3b) show the new center position of the eddy to be about 85 km west of Keahole Pt. From the time we first recognized a shift in the eddy's position, it travelled to the southwest, moving approximately 55 km in 10 days or indicating a speed of about 6 cm s^{-1} . During this time its size increased about two-fold.

Figure 5 presents dynamic height maps at three levels. The geostrophic swirl speeds at the surface (relative to 450 m) are as large as 1.3 m s^{-1} . The speeds at 150 m are as large as 0.5 m s^{-1} . Together with the drifter speeds of Table 1, which are regarded as surface geostrophic current, these numbers indicate that the reference level is a reasonable choice. The strength of the surface flow is consistent with our interpretation of it as geostrophic current; wind drift for typical wind speeds would be expected to be at most a few centimeters per second (e.g. NILER and KRAUS, 1977).

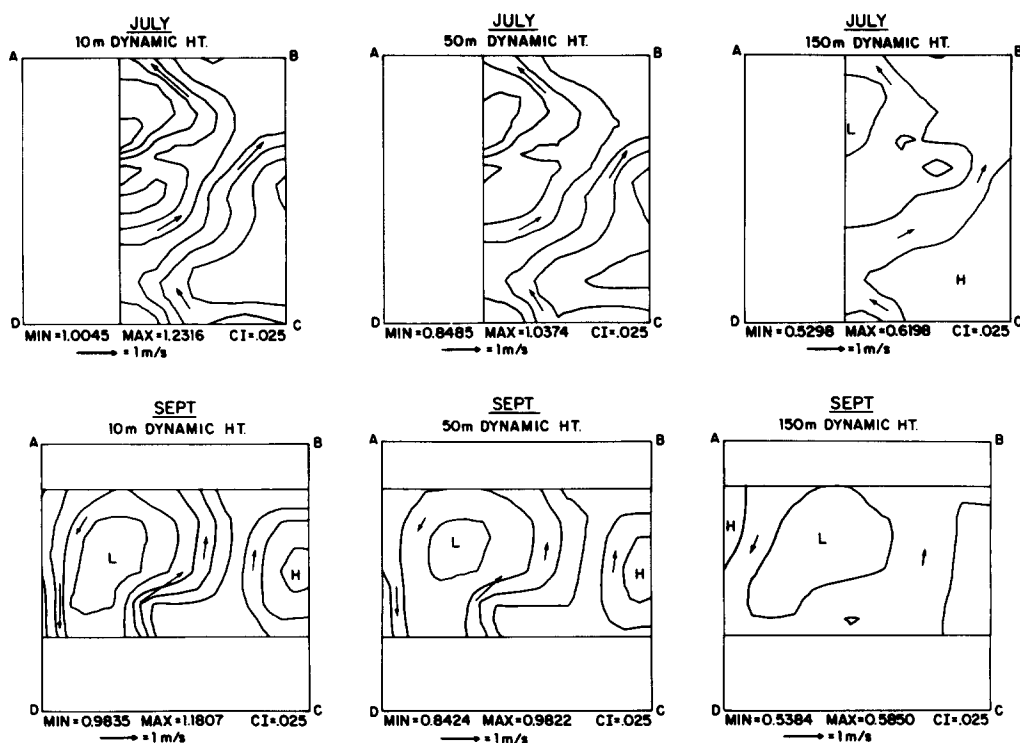


Fig. 5. Objective analysis of dynamic height fields (relative to 450 m) in July and September 1982. L = low pressure cell (cyclonic eddy). Arrows show speed and direction of flow. See Fig. 1 for domain location. The axis of the eddy appears essentially vertical: this is the case also for the deeper geostrophic flows not exhibited here.

BIOLOGICAL MEASUREMENTS

Plankton tows were taken in locations defined by physical measurements of the current field. Tows at locations 1, 2 and 3 were essentially in the eddy center and tows 4 and 5 in the intense swirl at about the same radial distance from the center, but at different azimuth angles (Fig. 3a).

Our choice of sampling methodology was dictated by available facilities; winches and an A-frame were not available on board of our small research vessel (7.6 m length). All tows were conducted during night-time between 2240 and 0530 h, times when the abundance of plankton near the surface is generally greatest (KING and HIDA, 1954; SHOMURA and NAKAMURA, 1969; NAKAMURA, 1967). Plankton were collected during night-time to maximize the likelihood of obtaining representative samples near the surface and to minimize problems associated with net avoidance and the deeper depth distribution of fishes in the daytime. Two plankton nets were hauled simultaneously at each of the 5 sites. Tow speed was between 1 and 1.5 kn. The 'surface' tow was at 0–2 m depth and the 'subsurface' tow was between 3 and 5 m. Nets were 1 m diameter with mesh size of 0.5 mm. Each net was equipped with a flow-meter. Station data for the plankton collections are given in Table 2.

Table 2. Station data for plankton collections

Depth of 24°C isotherm (m)	Time (h)	Date (1982)	Latitude/Longitude	
27	2242–2315	23 July	20°00'N	156°23.5'W
29	0325–0427	24 July	20°00.5'N	156°25'W
30.5	2315–0015	25 July	19°59'N	156°29.5'W
40	0102–0203	24 July	20°09.5'N	156°19.5'W
52	0443–0537	26 July	19°51.5'N	156°15.5'W

Each plankton sample was sorted for all ichthyoplankton. The total mass of zooplankton was estimated by displacement volume. Here we report the total number of fishes with emphasis on the abundance of defined developmental stages occurring in various locations in the cyclonic eddy current field. Larval fish developmental stages are defined following terminology used by LEIS and RENNIS (1983) as based upon the system of AHLSTROM *et al.* (1976) and MOSER and AHLSTROM (1970). See Table 3 for definitions. It is significant that definitions of the developmental stages are based in large part on the structures of the caudal fin and, thus related to the inferred relative swimming ability of the larvae.

The distributions of fish eggs and larvae and of zooplankton through the eddy suggest the following general patterns (Figs 6–8). The number of fish larvae was greatest in subsurface samples at every station. In general, both surface (0–2 m depth) and subsurface (3–5 m depth) sample data suggest similar trends. The total number of fish larvae was least nearest the eddy's center (Fig. 6). The difference between the number of fish larvae in surface and subsurface samples was least at the extremes of the eddy field (i.e. its center and edge) (Fig. 6). In contrast, the mass abundance of zooplankton (as estimated by displacement volume) nearest the eddy's center was greatest (Fig. 7). The most fish eggs were found near the eddy center (Fig. 8a).

The distribution of the larval developmental stages suggests that hatchlings were most abundant near the eddy center and that latter stages were most abundant in the main swirl of the eddy nearer its periphery (Fig. 8 and Table 4). The few data obtained to date do not allow statistical trends analysis. None of the larval fishes in the entire collection ($N = 513$) had yet developed into the settlement stage. However, this may also reflect

Table 3. Pelagic larva development stage classification (following the terminology of LEIS and RENNIS, 1983)

Hatchling:	Upon emerging from egg with yolk-sac, undifferentiated jaws, unpigmented eyes, pigment pattern dominated by dorsal melanophores.
Preflexion larva:	Begins at hatching, ends at start of upward flexion of notochord.
Flexion larva:	Begins with upward flexion of notochord, ends with hypural bones assuming a vertical position.
Postflexion larva:	Begins with full formation of caudal fin (hypural bones vertical), ends with attainment of full external meristic elements (rays and scales) and loss of temporary specialization for pelagic life.
Settlement stage:	Fish is morphologically and physiologically ready to adopt a substrate-associated lifestyle. Often but not always associated with larva to juvenile transition.
Juvenile:	Transition from pelagic larval habitat to adult reef habitat complete.

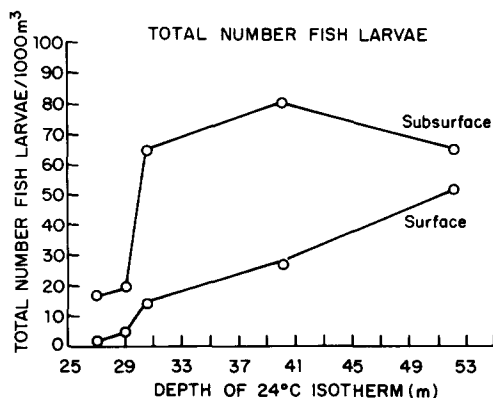


Fig. 6. The numerical abundance of all larval fishes along a transect from the center into the main swirl of a cyclonic eddy. Surface samples from 0 to 2 m depth and subsurface samples from 3 to 5 m depth. See text for details and Table 1 for station data. Location within the eddy is defined by depth of the 24°C isotherm, the shallowest values are in the eddy's center.

the capability of fish at that stage for eluding capture. If so, it is suggestive of their swimming ability.

The important result here is that the larval fishes generally increased in abundance from the eddy's center to periphery while other zooplankton exhibited the opposite trend. We emphasize that our data are only indicators of possible trends. We recognize that these few surface samples give only preliminary results, but ones which may serve as a basis for future research.

DISCUSSION

Every recent major review of marine fish ecology and life history has emphasized the lack of knowledge concerning the flux of free-floating eggs and larvae originating from coastal zones (e.g. EHRLICH, 1975; HELFMAN, 1978; JOHANNES, 1978; SALE, 1978, 1980b; BARLOW, 1981; LASKER and SHERMAN, 1981; NORCROSS and SHAW, 1984). What is known is that most coastal marine fishes spawn buoyant eggs which drift in surface currents.

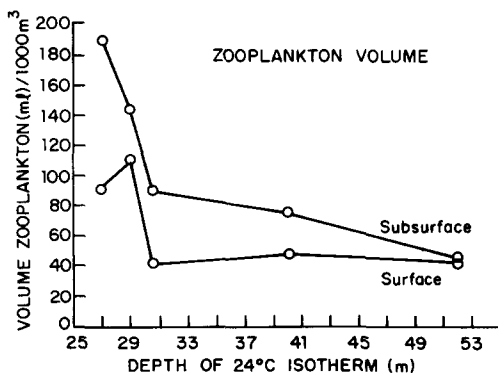


Fig. 7. Zooplankton displacement volume (ml) from the center to periphery of a cyclonic eddy. See Fig. 8 for details.

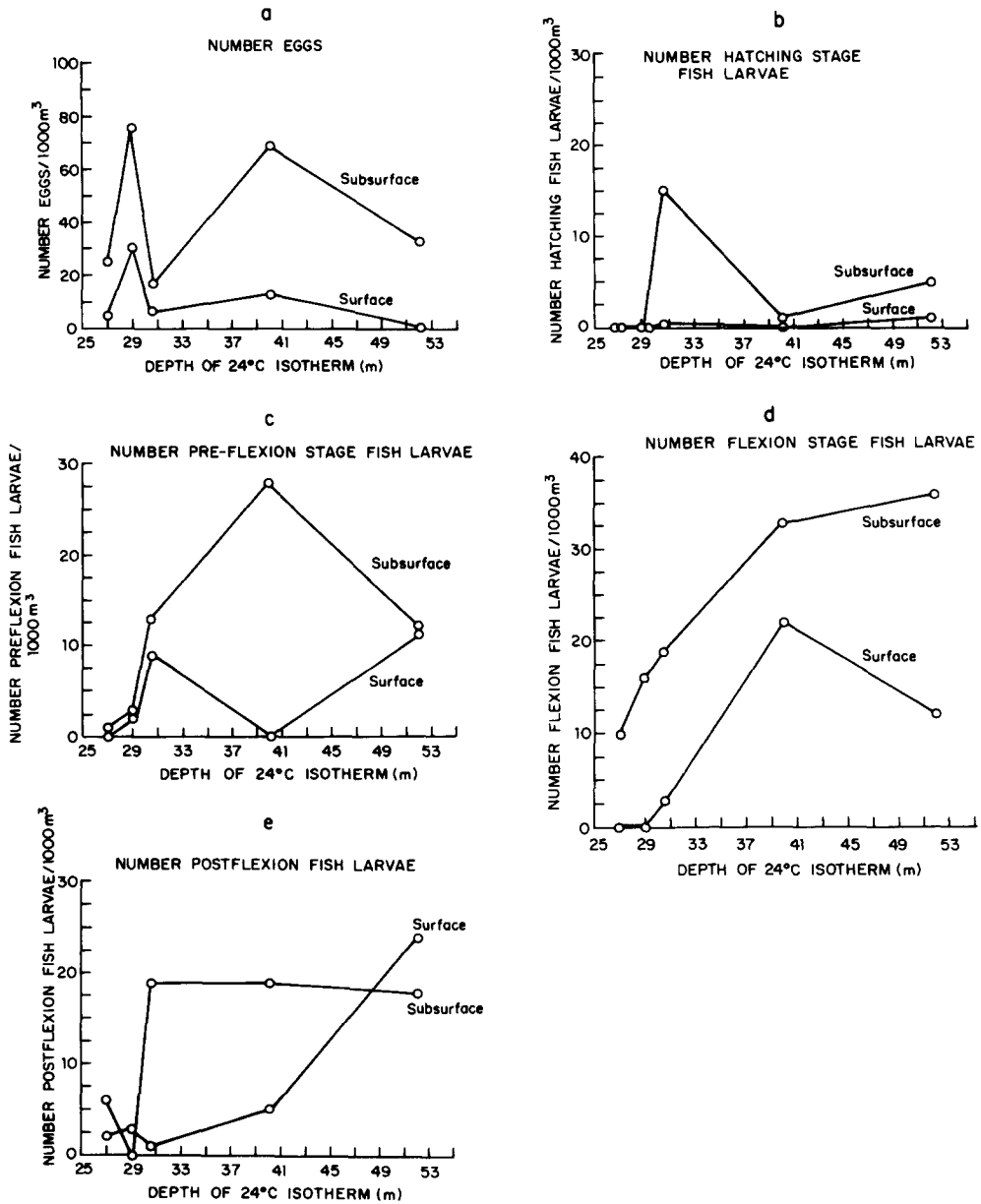


Fig. 8. Ichthyoplankton distributions across the cyclonic eddy. See Fig. 8 for details and Table 2 for definitions.

Table 4. *Abundance of larval fishes in a cyclonic eddy*

Depth of 24°C isotherm (m)	Plankton tow	Total volume seined (m ³)	Counts estimated per 1000 m ³									
			Volume zooplankton (ml)	Volume all fish larvae (ml)	Number (Fish?) eggs	Number all fish larvae	Number hatchlings	Number preflexion	Number flexion	Number postflexion	Actual number fish larvae	
27	Surface	1099	92	<0.01	5	2	0	0	0	2	2	
	Subsurface	1018	190	0.3	25	17	0	1	10	6	17	
29	Surface	615	112	0.7	76	5	0	2	0	3.3	3	
	Subsurface	608	145	0.2	31	20	0	3	16	0	12	
30.5	Surface	2036	43	0.05	7	14	0.5	9	3	1	29	
	Subsurface	1939	92	0.8	17	65	15	13	19	19	127	
40	Surface	1597	48	0.2	13	27	0	0	22	5	43	
	Subsurface	1439	76	0.7	69	81	1	28	33	19	117	
52	Surface	1547	43	0.4	1	52	5	12	12	24	81	
	Subsurface	1251	46	0.3	33	66	1	11	36	18	82	

Most fish eggs hatch within 36 h and the larvae remain with the plankton in offshore waters for weeks to months. Clearly, one important variable is the time scale of advection by currents relative to the minimum duration larvae must remain in the pelagic developmental phase. Significant questions include: (1) Are ichthyoplankton dispersed widely and haphazardly? (2) Can cohort groups be maintained? (3) Is passive drift the primary mechanism by which larvae are moved to and from coastal habitats?

The results presented herein demonstrate that a mesoscale cyclonic eddy can function as a larval fish nursery ground. The cyclonic eddy which appeared off Hawaii in July 1982 remained in the vicinity of the Kona coast for approximately 60 days, during the final peak of the fish spawning season. The mean duration of the pelagic larval stage for several Hawaiian fish species has been estimated at 49.1 ± 10.3 days ($N = 15$ spp.; BROTHERS and THRESHER, 1985). Thus, the eddy remained nearshore long enough for a variety of reef fishes to complete planktonic larval development.

The drift track and general domain of entrainment of reef fish eggs and larvae by the cyclonic eddy are suggested by the current drogue trajectories. Current drogues deployed near sites where fishes spawn drifted offshore and into the eddy. Drogues deployed in offshore waters about 30–50 nm south off the eddy's center also were entrained. All of the drogues circulated within the general confines of the eddy field and sometimes drifted within several km of shore. When the eddy finally moved away from the island it presumably also carried resident plankton along with it. These results support the hypothesis that ocean eddies can retain ichthyoplankton near islands.

These drogue tracks have interesting biological implications. The trajectories of drogues 1 and 2 deployed on 17 July indicate that the mesoscale eddy flow sweeps up the nearshore and reef region. They demonstrate how plankton originating over shallow waters can be swept into an offshore eddy, but also that originally adjacent parcels of water may have quite different fates.

The four drogues deployed on 21 July (two shown, Nos 3 and 4) demonstrate how plankton adrift in offshore waters may be swept into a cyclonic eddy. The return of one of these drogues very close to shore, shows how passive drift may bring plankton from offshore to nearshore again.

The 25 July drogue (No. 5) strikingly illustrates that plankton or other material located at the center of the eddy can remain trapped for almost 2 months.

The 2 September drogue (No. 6) shows how an eddy can sweep a drifter around in its main swirl, bringing the drifter nearshore again (in about 6 days) if the eddy remains stationary and carrying the drifter offshore as the eddy moves away.

Surely, passive drift will determine where and how quickly truly planktonic organisms, eggs and the earliest stage (i.e. non-swimming) fish larvae are distributed. It seems possible, however, that latter-stage larvae may possess sufficient swimming ability to orient themselves to currents. To explore these questions, we analyzed the distribution and abundance of fish larvae according to developmental stage. Developmental stage is assumed to translate to swimming ability although this is unknown. The latter stages of postflexion and settlement which are defined in part by completely developed fins are presumed to be the best swimmers. These larvae were most abundant in the outer swirl of the cyclonic eddy.

Eddies appear to be common features in Hawaiian waters. PATZERT (1969) found a correlation between the trade wind field; he also noted that eddy generation and eddies occurred at all times of the year behind the island of Hawaii except during periods of

slack-wind conditions. When winds were strongest, eddies formed in the lee of other islands, especially Oahu and Kauai.

We also observed that the outer swirl of this eddy and others previously investigated swept up and over the reef edges. When present the mesoscale currents swamped the coastal tidal flow. They provide a very effective cross-shore transport mechanism, carrying material both off and onto the reefs. In comparison with PATZERT (1969), our eddy was strong but not exceptional with regard to swirl speed, thermocline shear, isothermal doming and generation time.

The Hawaiian Archipelago stretches for about 2575 km and has 18 islands. The cyclonic eddy is a dominant ocean mesoscale feature, but many other features occur with considerable space time variability. The eddy currents sweep up onto and off of the reefs, transporting biological material. Eggs can be carried into entrainment centers and retained long enough to mature. Subsequently they can be returned to the reefs by the natural variability of the mesoscale current system. They may be returned to the reef of origin but of course could be returned elsewhere and to another island in the archipelago. Other eggs will of course be swept out to sea by the mesoscale currents and not survive. It would seem reasonable that the reproductive strategy of marine animals could reflect to some extent these transport mechanisms which are of great importance in their life cycle. To the extent that a mesoscale feature has a regularity (e.g. seasonality) to its occurrence because of its formation mechanism, then there may be an important link to the periodicity of the spawning and recruitment of species taking advantage of such features.

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