

# Influences of oceanographic and meteorological features on reef fish recruitment in Hawai'i

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**ABSTRACT:** Larval fish recruitment is generally highly variable in space and time, and can significantly influence adult population abundance, density and distribution, as well as community structure in coral reef systems. We investigated relationships between reef fish recruitment (data from the West Hawai'i Aquarium Project) and oceanographic and meteorological variables (measures of eddy presence and frequency, El Niño Southern Oscillation, sea surface temperature, sea surface height, chlorophyll *a* concentration and rainfall). We compared these variables at different time scales — monthly and annually — to substantiate 1 of 3 possible hypotheses about the relationship between eddies and other oceanographic features and fish recruitment: (1) they are positively correlated, indicating that eddy activity could enhance recruitment; (2) they are negatively correlated, indicating that eddy activity may reduce or inhibit recruitment; and (3) they are not correlated, indicating that eddy activity has no impact on recruitment. We found several potential linkages generally supporting the hypothesis that eddies negatively correlate with fish recruitment. In contrast to previous work, we found significant negative correlations in annual patterns of cold-core mesoscale eddies and young-of-the-year totals on the west coast of the island of Hawai'i. We also investigated time lags between monthly recruitment data and oceanographic data several months earlier, consistent with planktonic larval duration of *Zebrafish* *flavescens* and *Ctenochaetus strigosus*; these phase shifts also produced negative correlations. Our results are exploratory and are only correlations, and thus do not suggest causation; further exploration is needed to substantiate the possibility that eddies have a negative influence on reef fish recruitment. However, these results do call into question that eddies in west Hawai'i have a positive impact on fish recruitment, a theory that has persisted in the literature for nearly 30 yr.

**KEY WORDS:** Mesoscale eddy · Planktonic fish larvae · Fish replenishment area · FRA · Marine protected area · MPA · West Hawai'i Aquarium Project · WHAP

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## INTRODUCTION

Conservationists and fisheries scientists alike have long had a goal of understanding the dynamics of fish recruitment, which is generally highly variable in space and time. Variation in larval recruitment can significantly influence population abundance, den-

sity and distribution, as well as community structure in coral reef systems (Danilowicz 1997). With the increasing use of marine protected areas (MPAs) as a fisheries tool to restore stocks (Worm et al. 2009), there is also increased interest in determining the influence of MPAs relative to other drivers of recruitment variability.

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To address fishery declines and reduce user conflict on the Kohala–Kona–Ka‘u (west, leeward) coast of Hawai‘i (hereafter, West Hawai‘i), 9 fish replenishment areas (FRAs) were established in 1999, closing 27.8% of the coastline to aquarium fishing, and bringing the total portion of the coastline closed to aquarium fishing (i.e. including existing closed areas) to 35.2% (Tissot et al. 2004). In parallel, the West Hawai‘i Aquarium Project (WHAP) was established to conduct scientific research and monitoring on the effectiveness of this network of MPAs (Tissot et al. 2009). A recent analysis of yellow tang *Zebra-soma flavescens*, the most heavily harvested species in West Hawai‘i, showed a significant increase in juveniles—the main targets of the fishery—within closed areas, and of adults not only within sites closed to fishing but also in ‘boundary areas’ within 1 km of MPA borders, whereas densities of juveniles have decreased by 45% in areas open to fishing (Williams et al. 2009).

Ocean circulation off the West Hawai‘i coast is often strongly influenced by the presence of energetic mesoscale (50 to 150 km in diameter) cyclonic and anticyclonic eddies (Patzert 1969, Lumpkin 1998). Although the mechanisms of formation and propagation of these lee eddies are still a matter of debate (Calil et al. 2008), a key forcing factor, at least of the cyclonic eddies, appears to be the northeast trade winds as they pass between the islands of Maui and Hawai‘i (Lumpkin 1998, Dickey et al. 2008). The cold-core, cyclonic eddies are important agents in bringing nutrient-rich deeper waters to the euphotic zone and hence increasing biological activity (Lobel & Robinson 1986, Seki et al. 2001, Bidigare et al. 2003, Dickey et al. 2008, Kuwahara et al. 2008, Landry et al. 2008, Mahaffey et al. 2008, Rii et al. 2008). This increased nutrient flux, particularly within the oligotrophic subtropical gyre waters of the Hawaiian Islands, could potentially increase survival and subsequent recruitment of coral reef fishes if the eddy persists close to the shore long enough for the fish larvae to complete their development and return to reefs (Limouzy-Paris et al. 1997). In some systems, such as the Kuroshio, eddies are believed to assist larval feeding and transport (Nakata et al. 2000, Kasai et al. 2002), and on the Great Barrier Reef they may affect larval dispersal and recruitment (Wolanski & Spagnol 2000, Burgess et al. 2007). However, if larvae are concentrated in an eddy along with their predators (Seki et al. 2002) or are entrained in an eddy that moves far offshore, recruitment could potentially decrease (Jones 1968).

In Hawai‘i, mesoscale eddies can capture fish larvae from reefs and persist long enough to influence

pelagic larval development (Lobel & Robinson 1988). Some researchers (Lobel & Robinson 1983, Lobel 1989, 2011) have suggested that peak reproduction in Hawaiian reef fishes takes place during the months when mesoscale eddies are most likely to occur, although others (Flament et al. 1996) have said the timing of eddies is essentially random.

In addition to mesoscale eddies, other potential influences on fish recruitment and seasonal spawning patterns include water temperature (Balch et al. 1999), rainfall (Friedlander & Parrish 1998), timing of the spring algal bloom (Platt et al. 2003) and chlorophyll concentrations (Polovina et al. 2001). In this study, we examine possible effects of these variables on larval recruitment, especially whether mesoscale eddy activity is correlated with the reproductive period of fishes, because this may affect future planning and management of MPAs in Hawai‘i. Specifically, we investigate whether larval recruitment of coral reef fish in West Hawai‘i is correlated with monthly and annual variation in mesoscale eddies, as measured by sea surface temperature (SST) and sea surface height (SSH) identified using satellite data. We used SST and SSH because they are good parameters to use for eddy identification in this region (Polovina & Howell 2005, J. Polovina pers. comm.) and globally (Fu et al. 2010).

We also explore possible correlations between recruitment and El Niño activity (because fishermen in West Hawai‘i have used these events as a predictor of interannual *Zebra-soma flavescens* recruitment, assumed to be more productive during El Niño events) and between recruitment and productivity (as measured by chlorophyll concentration and rainfall, which would cause increased nutrient runoff from land). We investigate relationships between predictor and response variables to substantiate one of 3 possible hypotheses about the relationship between eddies and other oceanographic features and fish recruitment: (1) they are positively correlated, indicating that eddy activity could enhance recruitment; (2) they are negatively correlated, indicating that eddy activity may reduce or inhibit recruitment; and (3) they are not correlated, indicating that eddy activity has no impact on recruitment.

Variable environmental and oceanographic conditions may influence pelagic larval development, a stage that could last from weeks to months (Victor 1986, Thresher et al. 1989), and food availability (Shima & Swearer 2009), thus influencing future recruitment several months hence (Sponaugle & Pinkard 2004, Sponaugle & Grorud-Couvert 2006). Therefore, we also investigated phase shifting the data, i.e.

examining correlations between fish recruitment data and the preceding months' oceanographic data. Finally, as we were skeptical of the assertion of seasonal peak eddy formation during peak fish reproduction (Lobel & Robinson 1983, Lobel 1989), we re-examined the data behind those claims. These investigations will further our understanding of how oceanographic and meteorological features influence reef fish recruitment and potentially eliminate misconceptions that have persisted in the literature for nearly 30 yr.

## MATERIALS AND METHODS

### Data sources

Postlarval recruits were counted at each of the 23 WHAP survey sites (including 9 FRAs, 5 reference sites [MPAs established prior to creation of the FRA network] and 9 sites open to fishing) (Tissot et al. 2004) (Fig. 1) from March 1999 through November 2010, following the monitoring protocol described by Tissot et al. (2004), which included 4 to 6 visual surveys annually on four 25 × 4 m transects at each site.

Eight-day and monthly averages of SST and SSH imagery, sub-scened to 18.5 to 21.5° N, 155 to 158° W, were obtained from NOAA's CoastWatch program. SSTs were analyzed from 9 km resolution Advanced Very High Resolution Radiometer (AVHRR) Pathfinder (January 1999 to December 2002) and AVHRR GAC (January 2002 to December 2010 provided by NOAA OceanWatch—Central Pacific, <http://oceanwatch.pifsc.noaa.gov/>) data. SSHs were analyzed from 30 km resolution AVISO satellite data ([www.aviso.oceanobs.com/](http://www.aviso.oceanobs.com/)) gathered from January 1999 through December 2010 by the TOPEX/Poseidon and Jason-1 altimeters. Global 8-d averages of Pathfinder Version 5.0 (PFV5) night-time all-pixel SST imagery, and the corresponding overall quality flag files, were obtained for January 1999 to December 2009 from the National Oceanographic Data Center ([www.nodc.noaa.gov/SatelliteData/pathfinder4km](http://www.nodc.noaa.gov/SatelliteData/pathfinder4km)). Chlorophyll *a* (chl *a*) concentrations were calculated for the study area from the 4 km resolution MODIS sensor onboard the NASA Aqua satellite (March 2000 to November 2010; <http://modis.gsfc.nasa.gov/>). Mean monthly rainfall data (January 1999 to December 2010) were provided by National Weather Service (NWS) weather stations ([www.nws.noaa.gov/](http://www.nws.noaa.gov/)) on the west coast of Hawai'i: UPLH1, KASH1, WIHH1, HAUH1, KLEH1, KMUH1, PHAH1 and PPLH1 (rainfall gauge summary location maps: [www.prh.noaa.gov/hnl/pages/rain\\_summary.php](http://www.prh.noaa.gov/hnl/pages/rain_summary.php)), plus Honomalino (W. J. Walsh unpubl.

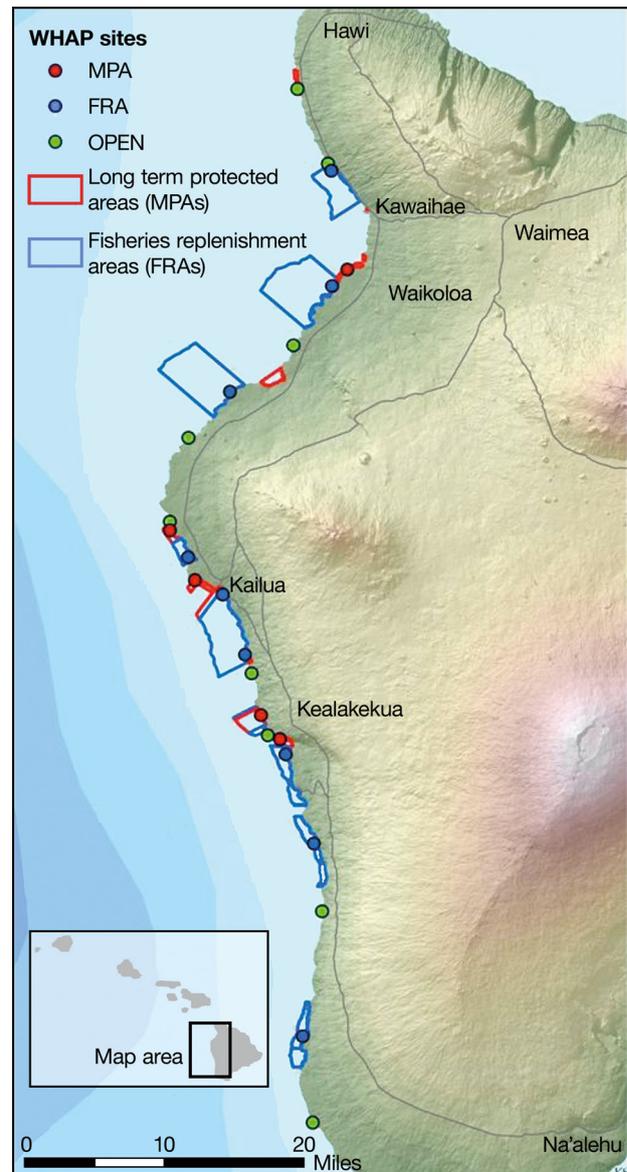


Fig. 1. West Hawai'i Aquarium Project (WHAP) survey sites along the West coast of Hawai'i

data). Lastly, NOAA Climate Prediction Center's Oceanic Niño Index (ONI) was used as a measure of the El Niño Southern Oscillation (ENSO), which is based on SST departures from average in the Niño 3.4 region (5° S to 5° N, 120 to 170° W) ([www.cpc.ncep.noaa.gov/products/analysis\\_monitoring/ensostuff/ensoyears.shtml](http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml)).

### Annual variation

To examine variations in annual recruitment and eddy activity, the annual young-of-the-year (YOY)

totals were calculated for the 5 most abundant species (*Zebrasoma flavescens*, *Ctenochaetus strigosus*, *Acanthurus nigrofuscus*, *Chaetodon multicinctus* and *Thalassoma duperrey*), plus those species combined. Because we were interested in recruitment on the scale of the entire management area, all sites and transects were pooled for analysis.

Annual eddy activity was based on a visual determination of eddy presence based on 8 d images of SST and SSH (sources above). Images were visually interpreted for temperature and altimetry fluctuations (Fig. 2 for color ramp and scale). This process, although time consuming, has been identified as a valid method for identifying eddies (de Souza et al. 2006, D'Alimonte 2009). A clear circular or elliptical SST (e.g. Fig. 2A) or SSH (e.g. Fig 2B) anomaly off the Kona coast persisting in approximately the same location in at least 2 consecutive 8 d images was recorded as an eddy. The number of 8 d images per year where eddies were present was recorded as the number of eddy-weeks. SSH images show contour lines (isopleths) of counterclockwise or clockwise direction of water flow, so both cyclonic and anticyclonic eddies were identified, whereas the SST images only show cyclonic (cold-core) eddies clearly. For each data frame in which an eddy was present, we estimated the following: temperature (°C) and height (cm) differential within and outside of the eddy (maximum difference between center and edge of eddy as determined by color differential [SST] or isopleths [SSH]), average diameter of the eddy and nearest distance to shore from the edge of the eddy (in pixels). We also created an expression of the 'influence' of each eddy by multiplying its size (in pixels) by the difference in temperature (°C) or height (cm) from the mean and dividing by the nearest distance to shore (in pixels) to provide quantitative differences between eddies.

Annual averages of chl *a* concentrations, the annual winter chl *a* 'algal bloom' (average concentration from November to February) and annual ONI and rainfall averages were calculated from monthly averages for analysis (sources above).

### Monthly variation

To examine finer-scale monthly variation in fish recruitment, we used recruit data from *Zebrasoma flavescens* and *Ctenochaetus strigosus*, as they have similar reproductive timing and are the most commonly occurring species, as well as the total of all recruits summed. All sites surveyed within a given

month were pooled for analysis. We then calculated moving 3 mo averages to smooth the data. This was necessary to make monthly comparisons, as some months had no WHAP surveys conducted. We recognize the potential risk of transferring uncertainty from the unsmoothed to smoothed data, which could yield smaller p-values with narrower confidence intervals.

Several methods were used to estimate monthly eddy activity (but not visual eddy estimation from SST and SSH satellite imagery) and other oceanographic features: standard deviation, mean monthly averages and monthly anomalies.

For standard deviation, the global PFV5 SST and flag files were sub-scened to the region defined above. Regional SST values were quality controlled by masking pixels with a corresponding overall quality flag value of less than 5 (Kilpatrick et al. 2001). The standard deviation of each of these images was computed. Polovina & Howell (2005) indicate that this measurement can be used as an index of cyclonic eddy activity. The resulting 8 d time series of SST spatial variance was then converted to a monthly time scale.

For mean monthly averages, we constructed monthly time series of the mean spatial SST, SSH and chl *a* concentrations, mean monthly rainfall for the west coast of Hawai'i and ONI (based on 3 mo running averages) values using the sources above.

For monthly anomalies, we calculated a monthly time series of anomalies from mean spatial SST, SSH and chl *a* concentrations. We determined the 12 yr mean for each calendar month of each variable over the entire survey period (1999–2010), and then subtracted this overall mean value from each monthly mean (e.g. January 2005 value – mean January 1999–2010 value = January 2005 anomaly).

### Analyses and phase shifts

We calculated multiple Spearman's correlations on annual and monthly data to determine the relationships between oceanographic and meteorological features and larval recruitment in Hawai'i (Tables 1 & 2 for list of variables and annual values). We also explored generalized linear models (GLMs; Poisson distribution and log-link function with overdispersion parameter included) to attempt to identify a more complete picture of how multiple variables are related to reef fish recruitment. For monthly data, several of the oceanographic variables were correlated, so we conducted a principal component analy-

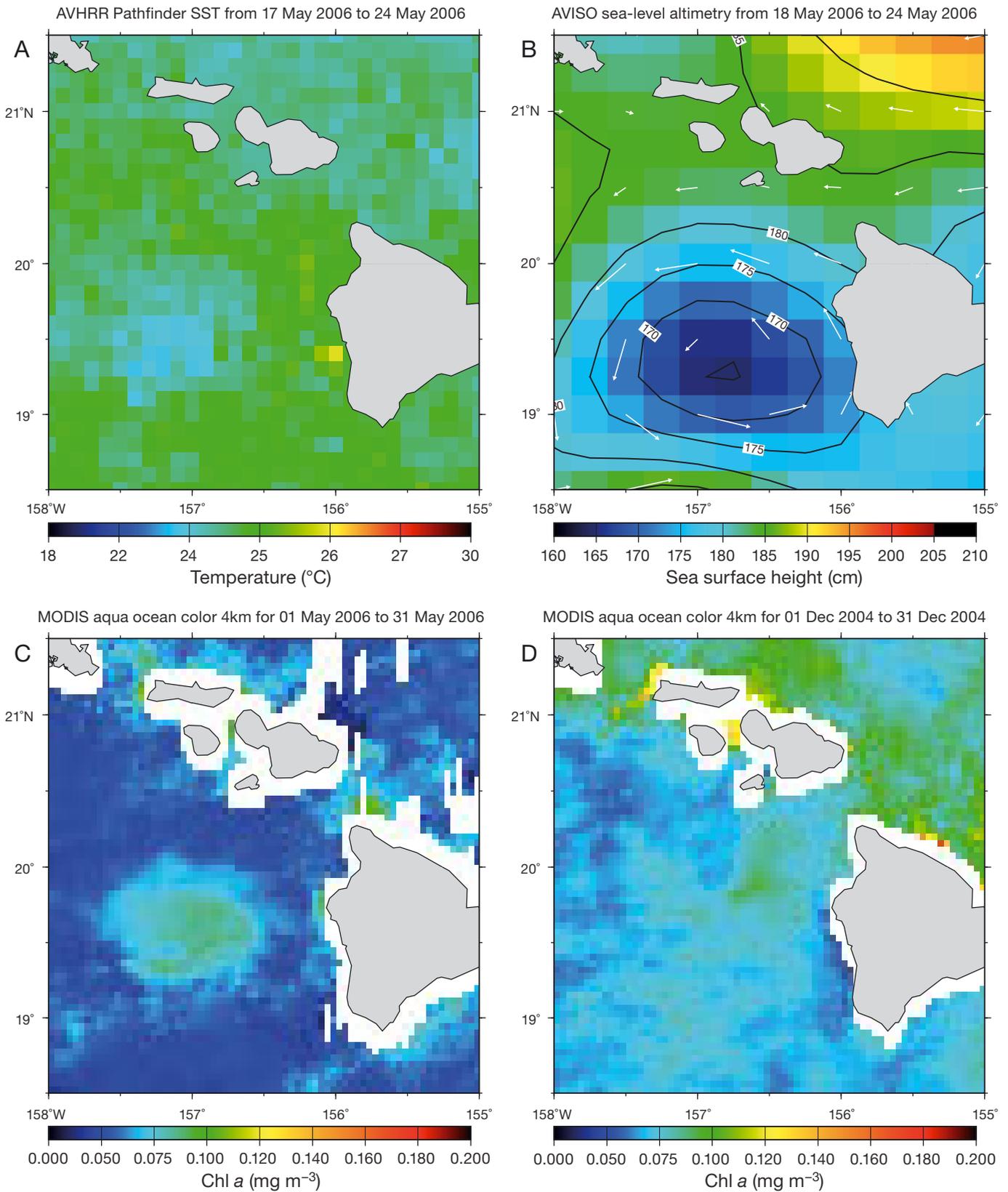


Fig. 2. Representative images showing (A) sea surface temperature (SST), (B) sea surface height (SSH) and (C) chl a, from approximately the same time period in May 2006, and (D) chl a during a winter bloom (December 2004); note that chl a images are monthly whereas the others are weekly

Table 1. Summary annual data of fish recruitment (young-of-the-year, no. ind. at WHAP survey sites) for the top 5 most abundant species (*Zebrafish flavescens*, *Ctenochaetus strigosus*, *Acanthurus nigrofuscus*, *Chaetodon multicinctus* and *Thalassoma duperrey*), individually and summed

Species	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
<i>Z. flavescens</i>	554	405	1300	4080	2678	1458	2296	507	1387	968	4057	735
<i>C. strigosus</i>	388	387	2089	3652	1911	579	2271	494	1080	1103	4020	570
<i>T. duperrey</i>	688	556	570	479	513	266	174	162	309	244	393	298
<i>C. multicinctus</i>	155	41	68	99	524	342	523	207	434	330	396	253
<i>A. nigrofuscus</i>	62	35	116	47	563	251	584	252	481	269	759	126
Total	1847	1424	4144	8375	6189	2896	5848	1622	3691	2914	9625	1982

Table 2. Summary annual data of several measures of eddy activity, and other oceanographic and meteorological variables. Means are presented  $\pm$  SD. Blank cells indicate years in which data were not available for a given variable. SSH: sea surface height; SST: sea surface temperature

	Eddy activity measures			Other variables			
	Total eddies (SSH/AVISO, visual; no. wk yr <sup>-1</sup> )	Cold-core eddies (SSH/AVISO, visual; no. wk yr <sup>-1</sup> )	Cold-core eddies (SST/Pathfinder, visual; no. wk yr <sup>-1</sup> )	Mean monthly rainfall (cm)	Mean monthly chl <i>a</i> (mg m <sup>-3</sup> )	Chl <i>a</i> bloom of previous year (mg m <sup>-3</sup> )	Oceanic Niño Index average (°C)
1999	30	9	16	3.036 $\pm$ 1.068			-1.058 $\pm$ 0.264
2000	34	26	11	3.019 $\pm$ 2.171	0.092 $\pm$ 0.030		-0.742 $\pm$ 0.399
2001	39	14	7	3.275 $\pm$ 1.736	0.077 $\pm$ 0.014	0.095 $\pm$ 0.015	-0.117 $\pm$ 0.266
2002	13	9	17	3.509 $\pm$ 1.805	0.076 $\pm$ 0.009	0.1 $\pm$ 0.004	0.775 $\pm$ 0.528
2003	25	9	2	2.42 $\pm$ 0.916	0.08 $\pm$ 0.015	0.085 $\pm$ 0.007	0.475 $\pm$ 0.352
2004	20	5	0	3.821 $\pm$ 2.890	0.087 $\pm$ 0.019	0.106 $\pm$ 0.006	0.558 $\pm$ 0.268
2005	31	13	9	6.082 $\pm$ 1.676	0.064 $\pm$ 0.004	0.116 $\pm$ 0.008	0.208 $\pm$ 0.406
2006	21	18	11	4.108 $\pm$ 2.812	0.066 $\pm$ 0.005	0.065 $\pm$ 0.002	0.25 $\pm$ 0.622
2007	30	16	19	3.548 $\pm$ 2.806	0.065 $\pm$ 0.005	0.064 $\pm$ 0.008	-0.3 $\pm$ 0.627
2008	23	10	9	3.052 $\pm$ 1.873	0.071 $\pm$ 0.011	0.065 $\pm$ 0.010	-0.558 $\pm$ 0.523
2009	24	8	10	3.01 $\pm$ 1.312	0.065 $\pm$ 0.015	0.082 $\pm$ 0.005	0.467 $\pm$ 0.855
2010	18	11	18	2.309 $\pm$ 1.150	0.064 $\pm$ 0.004	0.071 $\pm$ 0.002	-0.15 $\pm$ 1.206

sis (PCA; varimax orthogonal rotation using JMP) to produce a non-correlated subset of variables for use in analysis.

Because reef fish often have a pelagic larval phase lasting up to several months before settling at a recruitment site (Victor 1986, Thresher et al. 1989), we ran additional phase shift analyses to determine possible correlations of oceanographic and meteorological data shifted from 1 mo to 1 yr prior to recruitment data.

### Seasonal 'peak eddy formation'?

In his studies investigating ocean current variability and the spawning season of Hawaiian reef fishes, Lobel (1989, 2011) suggested that eddies do have an influence on larval recruitment and posited that peak eddy formation coincided with the peak season of reef fish reproduction, citing data from Patzert (1969). Because our data did not show this pattern,

we re-examined the original Patzert data with the inclusion of 2 measures of sampling effort: cruises per season and days spent at sea, which were not accounted for when calculating the number of eddies encountered per season (Lobel & Robinson 1983, Lobel 1989).

## RESULTS

### Annual variation

We found no statistically significant correlations between recruitment totals of all species combined and the number or intensity of eddies per year or any other oceanographic or meteorological variable (ONI, chl *a* concentrations, the size of the previous year's algal bloom, or annual mean rainfall) through preliminary analysis of Spearman's correlations with a Bonferroni correction applied to protect  $\alpha$  values (Table 3, Fig. 3). Similarly, there were no differences

Table 3. Spearman's pairwise correlation results of annual data comparing variables with young-of-the-year of the top 5 most abundant species. On an annual time scale, only the Oceanic Niño Index (ONI) is positively correlated with fish recruitment; however with Bonferroni correction ( $\alpha = 0.0083$ ), ONI is not significant

Variable	$\rho$	p
Temperature standard deviation ( $^{\circ}\text{C}$ )	0.1273	0.7092
Visual cold-core eddies (SSH/AVISO) >2 wk	-0.4930	0.1034
Visual cold-core eddies (SST/Pathfinder) >2 wk	-0.1926	0.5486
Mean monthly chlorophyll ( $\text{mg m}^{-3}$ )	-0.2000	0.5554
Mean monthly rainfall (cm)	-0.1049	0.7456
Oceanic Niño Index (ONI) average	0.6014	0.0386

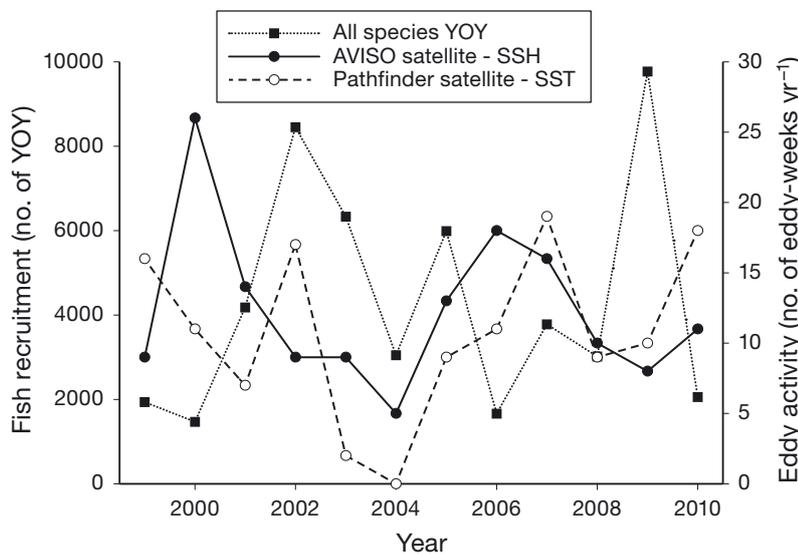


Fig. 3. Relationship between annual young-of-the-year (YOY) totals and number of weeks of eddy persistence per year, as estimated from sea surface height (SSH) and sea surface temperature (SST), determined using AVISO and Pathfinder satellite images, respectively. Only eddies that appeared in 2 or more consecutive 8 d satellite images were used for analysis (Table 3)

in significance of Spearman's correlations of individual species, with the exception of the *Zebrasoma flavescens* and ONI relationship ( $\rho = 0.75$ ,  $p = 0.0051$ ). However, when multiple variables were used to construct a GLM of YOY recruitment, we found that the number of cold core eddy-weeks per year (as estimated visually by SSH from Aviso satellites) and rainfall were negatively correlated with the top 5 species summed YOY (Table 4).

### Monthly variation

The most abundant juvenile recruits were *Zebbrasoma flavescens* and *Ctenochaetus strigosus*, ac-

counting for over 70% of all recruits sampled. Peak recruitment for these species was distinctly seasonal, with a peak in June to August (Fig. 4A) (Walsh 1987, Bushnell et al. 2010). In contrast, we found no evidence of a seasonal pattern of eddy activity, although eddy timing and duration was variable (Fig. 4B). We found no significant correlations between monthly reef fish recruitment and eddy activity as measured by standard deviation or mean monthly SSH (Fig. 4, Table 5). Mean monthly SST did show positive correlations with the fish recruitment data, which is unsurprising considering peak recruitment occurs in Hawai'i during the warmer months of the year (Walsh 1987, Bushnell et al. 2010). Monthly chl *a* concentrations were negatively correlated with recruitment data, driven primarily by the increase in chl *a*, or algal bloom, during the winter months when recruitment is low (Fig. 2D). This negative correlation was not significant when winter months from the chl *a* data were excluded and Bonferroni correction was applied to account for multiple comparisons. Rainfall and ONI were not correlated with recruitment (Table 5). When factors from our PCA (Table 6) and season were used as explanatory variables in our GLM, Factors 1 and 4, consisting of chl *a* and temperature related variables, respectively, as well as season had significant effects

on variation of monthly recruits. As expected, the summer season had a positive correlation estimate. Factor 4 also had a positive parameter estimate, whereas Factor 1 was negatively related to monthly recruitment.

### Phase shifts

When we explored a variety of phase shifts (up to a 1 yr lag of recruitment behind meteorological variables), recruitment data for all species were significantly negatively correlated with two oceanographic variables (SSH and chl *a*) phase shifted 2 to 5 mo before the recruitment data (Fig. 5, Tables 5 to 7).

Table 4. Statistical results of annual data. Generalized linear model with summed 5 most abundant species (young-of-the-year) as the response variable, Poisson distribution and log-link function. Results show that increased presence of cold-core eddies and increased rainfall are negatively correlated with fish recruitment when the other listed variables are controlled for. Data for fish recruitment and oceanographic variables were collected from 1999 to 2010 and are pooled to obtain one annual value for each variable per annum

Model statistics		Estimate		
Negative log likelihood – full model		2.16088954		
Negative log likelihood – reduced model		15.587913		
Pseudo R <sup>2</sup>		0.86137		
$\chi^2$		26.854		
p		<0.0001		
df		6		
Variable statistics				
Predictor variable	Estimate	SE	$\chi^2$	p
Intercept	8.0969459	2.8460176	8.6468869	0.0033
Temperature standard deviation (°C)	6.1630868	5.1513474	1.3863508	0.239
Chl a concentration (mg m <sup>-3</sup> )	-7.523541	13.581113	0.3114266	0.5768
Visual cold-core eddies (SST/Pathfinder) > 2 wk	0.028004	0.0260729	1.1249928	0.2888
Mean monthly rainfall (cm)	-0.329661	0.1607756	4.4878259	0.0341
Visual cold-core eddies (SSH/AVISO) > 2 wk	-0.078121	0.029758	8.18341	0.0042

### Seasonal 'peak eddy formation'?

We found no indication of increased eddy presence coinciding with the peak season of recruitment (Fig. 6A). Likewise, although the Patzert (1969) data showed more eddies in the spring and summer than in the winter, the researchers spent nearly 3 times as many days at sea, on twice as many cruises during the spring and summer months. Of the 20 cruises included in the report, 8 occurred during the spring months, 8 during the summer and only 4 during the winter. Eddies were encountered on all cruises except one, occurring in the spring. Patzert (1969) recorded 15 eddies from January to May (spring), 14 eddies from June to August (summer) and only 5 eddies from September to December (winter); however, 99, 83 and 33 d were spent at sea in the region where eddies were detected during the spring, summer and winter, respectively. When accounting for days at sea and number of cruises per season, there was no difference in the number of eddies occurring during each season (days at sea:  $\chi^2 = 0.19$ ,  $p = 0.91$ ,  $df = 2$ ; cruises per season:  $\chi^2 = 2.00$ ,  $p = 0.37$ ,  $df = 2$ ; Fig. 6B).

## DISCUSSION

We found several potential links between eddy activity and fish recruitment, generally supporting the hypothesis that eddies negatively correlate with fish recruitment. Our results show negative correla-

tions both between annual fish recruitment and cold-core eddies (Table 4) and between oceanographic variables and fish recruitment 2 to 5 mo later (Fig. 4). Of particular interest is that *Zebrasoma flavescens* and *Ctenochaetus strigosus* spend approximately 2 mo in a planktonic larval phase (Eble et al. 2009), which corresponds to the time lag in correlation that we found between oceanographic variables and recruitment (Table 5).

These results are consistent with the hypothesis that eddies may entrain larvae as they move further offshore, reducing overall recruitment, and highlight possible starting points for future exploration of possible mechanisms. Late-larval fish are found in higher concentrations near the periphery of meso-scale Hawai'ian eddies, whereas more passive zooplankton such as fish eggs are found nearer to the center (Lobel & Robinson 1986), suggesting that those late-larval and early juvenile reef species that are capable of sustained swimming independent of the direction of the current (Leis & Carson-Ewart 2003) may be attempting to exit the eddy. However, maximum current speeds within a Hawai'ian eddy average 150 cm s<sup>-1</sup> (Lobel & Robinson 1986), more than double the maximum swimming speed of most reef fish larvae (Fisher 2005). Although larvae can sense nearby reefs using auditory (Wright et al. 2010) or olfactory (Miller-Sims et al. 2011) cues, westward movement of an eddy (Lobel & Robinson 1986) is likely to take larval fish outside the range of these sensory cues (Radford et al. 2011).

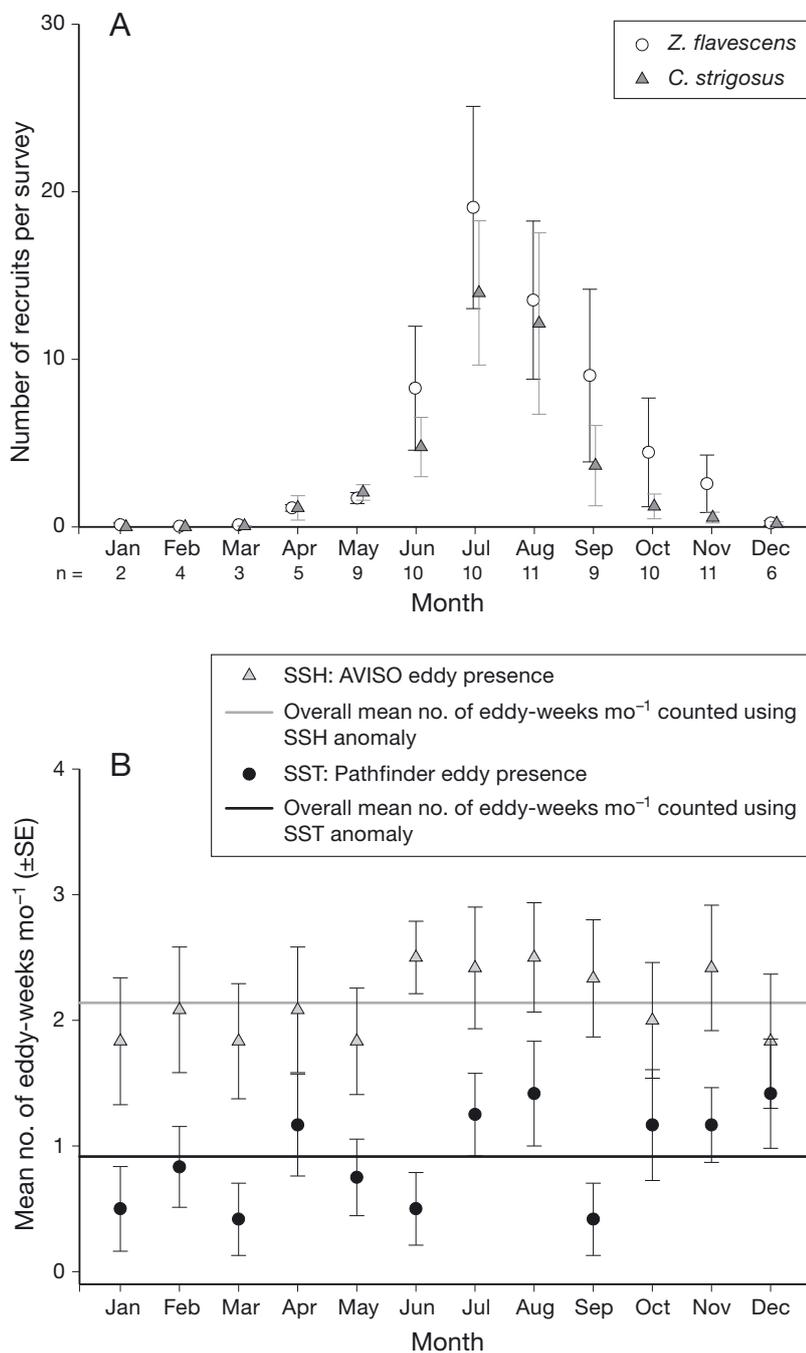


Fig. 4. (A) Recruit data for years 1999–2010 combined for a monthly mean ( $\pm$ SE) number of *Zebrasoma flavescens* and *Ctenochaetus strigosus* recruits per survey. n: number of years for which surveys were undertaken for a given month; winter and spring surveys were conducted less frequently than summer surveys. (B) Mean ( $\pm$ SE) number of eddy-weeks per month for years 1999–2010 determined using satellite images displaying sea surface height (SSH) (AVISO satellite, cold- and warm-core eddies) and sea surface temperature (SST) (Pathfinder satellite, cold-core eddies only). Horizontal lines represent grand mean number of eddies per month determined using satellite images displaying SSH (grey) and SST (black). Monthly Wilcoxon test of eddies SSH:  $\chi^2 = 4.54$ ,  $p = 0.952$ ,  $df = 11$ ; SST:  $\chi^2 = 15.70$ ,  $p = 0.153$ ,  $df = 11$  determined using satellite images displaying years.

ENSO events are known to influence the recruitment of pelagic fish and some nearshore reef fish in regions closer to the Niño 3.4 region in the Pacific (Meekan et al. 2001, Lehodey et al. 2006, Cheal et al. 2007). Our finding of enhanced *Zebrasoma flavescens* recruitment during El Niño events is counter to others' descriptions of decreased larval supply during warmer periods (e.g. Lo-Yat et al. 2011). Although the exact mechanism is unknown, El Niño events are known to influence regional trade winds (Cao et al. 2007) and cyclonic activity (Chu & Wang 1997), which can influence ocean currents and thus recruitment dynamics. El Niño events are also typically associated with a decrease in primary production (Kahru & Mitchell 2000, Lo-Yat et al. 2011, Park et al. 2011); however, our data showed no correlation between ONI and chl *a* concentration ( $R^2 < 0.0001$ ,  $p = 0.9717$ ). Further investigation into ENSO and fish recruitment is warranted.

Of course, these results are correlations, and do not indicate causation, and were not conclusive either at annual (Fig. 3, Tables 3 & 4) or monthly (Tables 5 & 6) time scales. However, the lack of positive correlations between any of several measures of eddies and fish recruitment in each of several metrics strengthens our argument that previous studies conducted in Hawai'i citing eddies as a positive influence on reef fish recruitment (Lobel & Robinson 1988, Lobel 1989, 2011) need to be reviewed. Our results suggest that eddies are not the primary force influencing fish recruitment, and may in fact have a negative influence.

Visual identification of an eddy's diameter (and therefore determination of temperature/height differentials and distance to shore) is subjective, as rescaling the color scale of imagery could influence the perceived size of an eddy; however, this

Table 5. Spearman's pairwise correlation results of monthly data without shifting and shifted by 2 mo comparing variables with average monthly fish recruitment (all species summed, 3 mo moving averages). Sea surface temperature (SST) is positively correlated whereas both chl *a* variables are negatively correlated with fish recruitment when data are not shifted. When recruitment data are shifted to 2 mo following oceanographic data to account for planktonic larval duration of most common species, SST, sea surface height (SSH), chl *a* and rainfall are all negatively correlated with fish recruitment. With Bonferroni correction, only p-values >0.0071 are significant (\*)

Variable	— No shift —		— Shifted 2 mo —	
	$\rho$	p	$\rho$	p
Temperature SD (°C)	0.1361	0.1704	0.1536	0.1214
Average SST (°C)	0.3663	<0.0001*	-0.2861	0.0023*
Average SSH (cm)	-0.1453	0.1281	-0.4425	<0.0001*
Mean monthly chl <i>a</i> (mg m <sup>-3</sup> )	-0.5055	<0.0001*	-0.5529	<0.0001*
Mean monthly chl <i>a</i> (bloom excluded; mg m <sup>-3</sup> )	-0.2877	0.0157	-0.3287	0.0027
Mean monthly rainfall (cm)	-0.1811	0.0572	-0.2087	0.0280
Oceanic Niño Index	0.1534	0.1081	-0.0018	0.9848

process has been identified as a valid method for identifying eddies (de Souza et al. 2006, D'Alimonte 2009). Each set of images had the same color scale for the entire 12 yr period, so the interpretation of the results overall should not be affected. One of our goals was to explore a number of possible avenues for further work, and our results corroborate the find-

Table 6. Oceanographic variables grouped into rotated principal components. Principal components analysis performed using JMP, varimax rotation. Number of factors were chosen based on visual inspection of the scree plot and eigenvalues ≥1. These factors correspond to F1 to F4 in Table 7

Factor	Variable	Rotated factor loading
1	Mean monthly chl <i>a</i> concentration (mg m <sup>-3</sup> )	0.987
1	Mean monthly chl <i>a</i> concentration – winter bloom excluded (mg m <sup>-3</sup> )	0.998
1	Chl <i>a</i> concentration anomaly (mg m <sup>-3</sup> )	-0.976
2	Mean monthly rainfall (cm)	0.978
2	Maui mean monthly rainfall (cm)	0.856
2	Hawaii mean monthly rainfall (cm)	0.893
3	Average SSH (cm)	-0.891
3	Temperature standard deviation (°C)	0.335
3	SSH anomaly (cm)	0.929
4	Oceanic Niño Index	0.785
4	Average SST (°C)	0.708
4	SST anomaly (°C)	-0.806

ings of others that have, in general, reported unpredictable and highly variable larval recruitment (Caselle & Warner 1996). Previous studies also suggest the presence of large variability in recruitment rates across biogeographic scales and emphasize the need for an improved understanding of larval responses to ocean circulation in the management and conservation of coastal ecosystems (Broitman et al. 2008). Ecological factors could also explain recruitment variation, including varying source populations (Claisse et al. 2009), post-settlement mortality (Hunt & Scheibling 1997) or habitat differences (Caselle & Warner 1996).

Clearly more investigation is needed to determine the causal effects, if any, of oceanographic events on recruitment. If oceanography or meteorology do affect recruitment in later months, understanding that might improve scope for conservation planning, including placement of marine reserves or FRAs, especially in areas with limited recruitment (including Hawai'i; Walsh 1987). For example, because larvae of benthic invertebrates

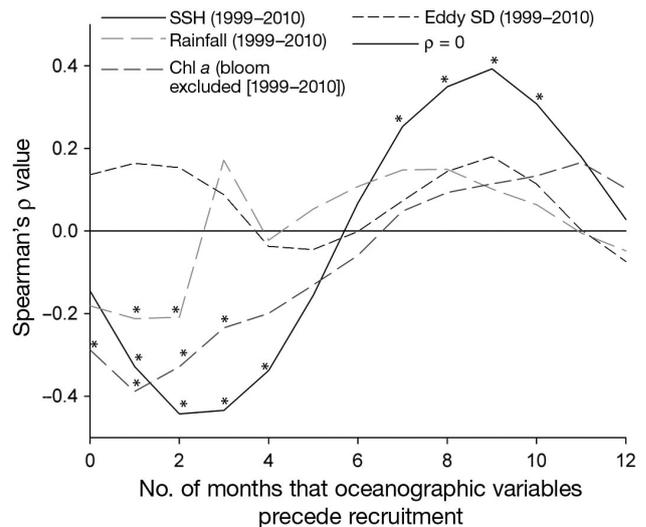


Fig. 5. Spearman's  $\rho$  value of correlation between phase shifted data for all fish recruits and different oceanographic variables (years of data collection in parentheses or brackets). All oceanographic data precede recruit data when shifted. Sections of lines denoted by asterisks show significant correlations ( $p < 0.05$ ) when compared with recruitment. Lines above the solid line at  $\rho = 0$  denote positive correlations, while those below the line designate negative correlations

Table 7. Statistical results of monthly data. Data for fish recruitment and oceanographic variables were collected from 1999 to 2010 and were pooled to obtain one monthly value for each data set. (A) Generalized linear model, not shifted, with number of recruits of all species as the response variable, Poisson distribution and log-link function. Results show that summer season, chl *a* anomaly, ONI and SST are positively correlated with recruitment, whereas increased chl *a* and temperature anomaly are negatively correlated with fish recruitment when other listed variables are controlled for. (B) Generalized linear model, oceanographic features occurring 2 mo prior to recruitment, with number of recruits of all species as the response variable, Poisson distribution and log-link function. Results show that summer season, chl *a* anomaly, ONI, SST and SSH anomaly are positively correlated with recruitment, whereas increased chl *a*, SSH and temperature anomaly are negatively correlated with fish recruitment when other listed variables are controlled for. Asterisks indicate variables that are significantly correlated at  $\alpha = 0.05$

Predictor variable	Estimate	Standard error	$\chi^2$	p
<b>(A) Model statistics — no shift</b>				
Negative log likelihood – full model	65.29			
Negative log likelihood – reduced model	128.58			
Pseudo R <sup>2</sup>	0.49			
$\chi^2$	126.575			
p	<0.0001			
df	6			
<b>Variable statistics — no shift</b>				
Intercept	2.4	0.11	211.25	<0.0001*
F1: chl <i>a</i> variables	-0.47	0.11	23.63	<0.0001*
F2: rainfall variables	-0.16	0.12	1.95	0.1626
F3: SSH variables and temperature standard deviation	0.12	0.07	2.6	0.1072
F4: SST variables and ONI	0.3	0.1	8.76	0.0031*
Season – Spring	-0.26	0.17	2.576	0.1086
Season – Summer	0.82	0.12	54.03	<0.0001*
<b>(B) Model statistics — shifted 2 mo</b>				
Negative log likelihood – full model	53.78			
Negative log likelihood – reduced model	109.27			
Pseudo R <sup>2</sup>	0.51			
$\chi^2$	126.575			
p	<0.0001			
df	6			
<b>Variable statistics — shifted 2 mo</b>				
Intercept	2.45	0.12	187.87	<0.0001*
F1: chl <i>a</i> variables	-0.36	0.12	11.54	0.0007*
F2: rainfall variables	-0.12	0.11	1.28	0.2582
F3: SSH variables and temperature standard deviation	0.22	0.09	6	0.0143*
F4: SST variables and ONI	0.24	0.11	5.44	0.0196*
Season – Spring	-0.12	0.19	0.42	0.5183
Season – Summer	0.95	0.13	62.52	<0.0001*

accumulate in the lee of headlands, including these areas in networks of marine reserves can enhance recruitment-limited adult populations (Mace & Morgan 2006). Possible future work could include targeted sampling studies of fish larvae off the Kona coast to determine the extent to which they are entrained in eddies and subsequently return to reef habitats. Increased recruitment has been suggested in prior studies (Lobel & Robinson 1988, Williams & English 1992, Franco et al. 2006), although we found no evidence that mesoscale eddies were more likely to occur or be absent during months of peak recruitment, and previous findings to that effect (Lobel 1989) did not take into account any measure of sam-

pling effort (the number of cruises or days at sea; Fig. 6).

The absence of definitive evidence of linked physical–biological processes in recruitment of new fishes in West Hawai'i supports the need for precautionary management of fish stocks, including the FRAs as established. Furthermore, existing data are clear: West Hawai'i FRAs are enhancing populations of *Zebrasoma flavescens* as well as the commercial fishery, demonstrating that conservation and protection of marine areas can help ensure sustainability and productivity of stocks (Tissot et al. 2004, Ortiz & Tissot 2008, Williams et al. 2009).

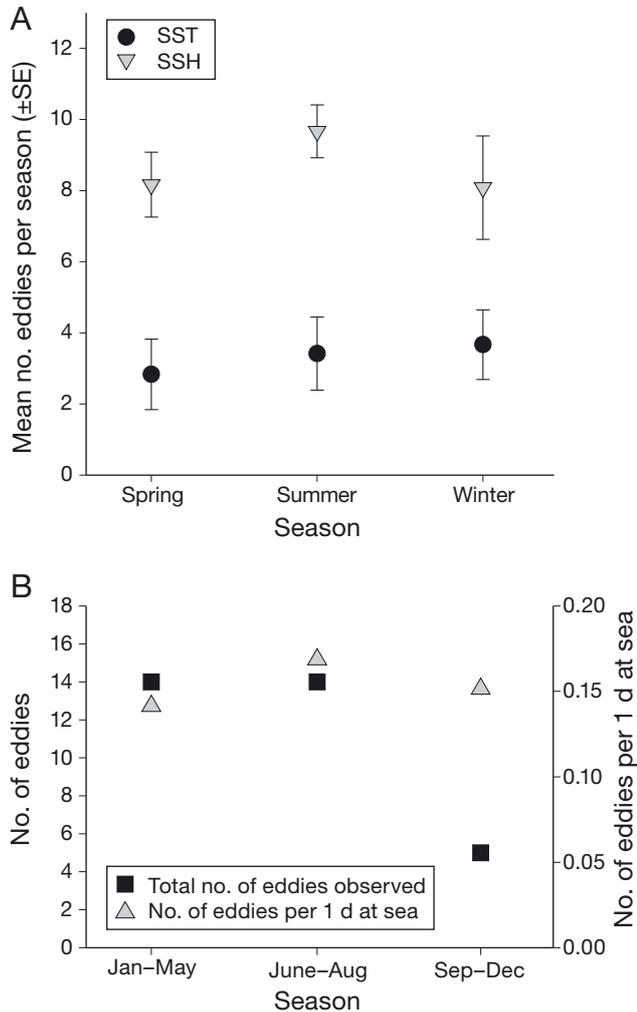


Fig. 6. (A) Mean number of eddy weeks per season for years 1999–2010 determined using satellite images displaying sea surface height (SSH; Aviso) and sea surface temperature (SST; Pathfinder). Wilcoxon test of eddies by season, 1999–2010, SSH:  $\chi^2 = 0.178$ ,  $p = 0.41$ ,  $df = 2$ ; SST:  $\chi^2 = 0.51$ ,  $p = 0.78$ ,  $df = 2$ . (B) Reanalysis of data from Patzert (1969) as reported in Lobel (1989). When accounting for days at sea, eddy presence does not coincide with the peak season of recruitment (Wilcoxon test of Patzert 1969 data reanalysis:  $\chi^2 = 0.19$ ,  $p = 0.91$ ,  $df = 2$ )

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