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Flyingfish (Exocoetidae) species diversity and habitats in the eastern tropical Pacific Ocean

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Abstract

Flyingfishes are large enough to eat zooplankton, small enough to be consumed by top predators, and therefore form a central mid-trophic component of tropical epipelagic marine food webs. Characterizing patterns of flyingfish abundance, distribution, and habitat preference have important implications for understanding both localized and generalized functions of marine ecosystems. The eastern tropical Pacific Ocean (ETP) supports many flyingfish species and their predators, yet no studies to date have identified oceanographic factors that define flyingfish habitats or estimate species richness and diversity at broad taxonomic and geographic scales. In this study, we analyzed 11,125 flyingfish representing 25 species and all 7 named genera, collected from the ETP over a 21-year period. We applied spatially-explicit analysis methods (ARCGIS, DIVA-GIS, MAXENT) and compared specimen locality data to remotely-sensed oceanographic data, and previously described oceanographic partitions. Our results show that *Exocoetus* is the most abundant genus (49%), and *E. monocirrhus* the most abundant species (32%) of flyingfishes in the ETP. Mean sea surface temperature was most important for defining flyingfish habitats (19.2–41.7%) and species richness (highest in the North Equatorial Current). Additionally, flyingfish species diversity was found to be highest in coastal regions of the study area (Shannon indices > 1.5). Together, these results provide unprecedented characterizations of a mid-trophic epipelagic community in an economically valuable region during a time when sea surface temperatures are predicted to increase as a result of global climate change.

Keywords

Epipelagic; Habitat Model; Maximum Entropy; Species Distribution Model

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INTRODUCTION

The tropical epipelagic zone is the surface layer of oceans (0–200 m) within 30° of the equator (Parin 1968). Despite the exceptional magnitude of the tropical epipelagic zone, which covers roughly 37% of the open ocean (Longhurst and Pauly 1987), overall species diversity is lower than in other similar-sized marine areas (Angel 1993). The large geographic ranges of epipelagic fishes, remoteness of regions they occupy, and high mobility of their movements, have resulted in a major gap in our basic understanding of epipelagic habitats. What determines the habitats of tropical epipelagic fishes, and how are these habitats best defined?

The eastern tropical Pacific Ocean (ETP) encompasses the waters of Central America from southern California (30°N) to Peru (20°S) and extends to approximately 150°W. This vast area supports some of the largest fisheries in the world (e.g., *Engraulis ringens*, *Dosidicus gigas*, *Thunnus albacares*), and has a distinct assemblage of marine mammals and seabirds susceptible to commercial fishing (Ballance, Pitman et al. 2006). Long-term surveys and remotely sensed data have aided the identification of oceanographic partitions within the ETP, based largely on patterns of primary productivity (Pennington, Mahoney et al. 2006). These oceanographic partitions are associated with the ecology of various organisms (e.g., zooplankton (Fernández-Álamo and Färber-Lorda 2006), seabirds and cetaceans (Ballance, Pitman et al. 2006)). However, the basic biology and ecology of other taxa in the ETP (e.g., epipelagic fishes) must be characterized to facilitate interpretation of mechanisms that influence species diversity in the region.

Flyingfishes are a particularly suitable model for investigating how oceanographic features may affect epipelagic fish habitats because they are restricted to surface waters (Nesterov and Bazanov 1986), and do not make long distance migrations (Parin 1968). Passive transport of early life stage individuals (Parin 1968), short generations (typically 1–2 years; (Steven, Oxentord et al. 1993)), and small home ranges (e.g. < 500 km² for *Hirundichthys affinis*; (Oxenford 1994)) indicate low migratory capabilities for flyingfishes. Remotely-sensed oceanographic measurements can be associated directly with the surface layer habitats of flyingfishes. As a central component of epipelagic food webs throughout tropical and subtropical regions of the world oceans (Parin 1968; Rau, Mearns et al. 1983), flyingfishes are important for advancing our overall understanding of mid-trophic marine ecology.

More than 50 species of exocoetids are currently recognized (22 species within the ETP; (Parin 1995)), making it one of the most species-rich lineages of epipelagic fishes. Morphological similarities among species and fast aerial gliding movements of individuals make flyingfishes difficult to identify *in situ* during observational surveys (Parin 1981; Parin 1983; Oxenford, Mahon et al. 1995; Churnside, Brodeur et al. 2009). Moreover, minor morphological differences between some species mean that increased scrutiny is required for accurate identification (Parin 1996; Parin and Belyanina 1998; Parin 1999; Parin and Shakhovskoy 2000; Parin and Belyanina 2002; Parin and Belyanina 2002).

In this study, we applied a combination of spatial analysis methods to a remarkably large dataset (11,125 identified and georeferenced flyingfish specimens collected throughout the ETP over a 21-year period) to characterize flyingfish habitats in the ETP. We first summarized the relative abundance of each species, and subsequently analyzed each of the 12 most abundant species using predictive distribution models based on 11 independent oceanographic variables. The overall species richness of flyingfishes in the ETP was also considered. Lastly, we estimated and plotted species diversity within our study area. This study provides a broad-scale description of flyingfish habitats including representatives of every known genus, and nearly half of known species.

MATERIALS AND METHODS

Study area, sampling, and specimen handling

Our study area was 20 million km² of ocean within the ETP, extending from southern California to Peru, and offshore to roughly 150°W (Fig. 1a). From 1986 to 2007, the NOAA Southwest Fisheries Science Center (La Jolla, CA, USA) conducted 32 scientific research cruises in the ETP (Appendix 1). Flyingfishes were collected during these cruises, providing an unprecedented opportunity to study species distributions, relative abundance and habitat preferences. Cruises were conducted between July and December (<1% in July; 20.4% in August; 27.4% in September; 28.4% in October; 22 % in November; 1.7% in December). Specimens of all sizes (adults, juveniles, and larvae) were collected at 2,491 sampling stations (Fig. 1a), along tracklines designed to systematically survey dolphin populations in the ETP. Flyingfish sampling stations began 1 h after sunset and usually lasted for 1 h. Adults were most common, and eggs were not sampled. To aid in detecting specimens, one or two deck-mounted spotlights were used to illuminate 50 m² of water next to the ship. Samples were collected by two researchers, each using a long-handled (8 m) dipnet with a basket 1 m in diameter and 1.5 m deep; net mesh size was <0.5 mm. Locality information (latitude and longitude) was recorded for each sampling locality using the shipboard navigation system.

After capture, all specimens were sacrificed using an ice bath and subsequently frozen in seawater. At the end of each research cruise, specimens were thawed, fixed in 4% formalin, rinsed, and preserved in alcohol (70% isopropyl or ethyl). Specimens were identified to species using published species descriptions and regional field guides (both for the ETP and west-central Pacific) (Parin 1961; Parin 1995; Parin 1996; Parin and Belyanina 1998; Parin 1999; Parin and Shakhovskoy 2000; Parin and Belyanina 2002; Parin and Belyanina 2002; Shakhovskoy 2007; Shakhovskoy and Parin 2010)). All specimens were catalogued at the Scripps Institution of Oceanography (USA), Los Angeles County Museum (USA), or Royal Ontario Museum (Canada).

Predictive species distribution models

MAXENT, v.3.3.3 (Phillips, Anderson et al. 2006; Phillips and Dudík 2008) is a widely-used software for producing predictive species distribution models. As inputs into MAXENT, we used two sets of data: (i) 11,125 identified specimens with cross-referenced “presence only” locality data (latitude and longitude) and (ii) oceanographic data for 11

variables measured within the ETP between the years of 1997 – 2010 and published in BioOracle (Tyberghein, Verbruggen et al. 2012). To ensure the robustness of these analyses, we only considered the 12 most abundant species each with a minimum of approximately 100 collected individuals (Table 1).

Predictor data for 11 environmental variables were compiled by Tyberghein et al. (Tyberghein, Verbruggen et al. 2012) and made available in BioORACLE, a comprehensive source of oceanographic data that covers the ETP to a resolution of 5 arc minutes. These 11 variables were prioritized to ensure oceanographic and biological independence after scrutinizing a total of 23 variables and retaining only the variables that produce unique response curves. Specifically, the following parameters were used in MAXENT: use of a random seed, a random test percentage of 50, a regularization parameter of 1, a maximum of 10,000 iterations, a convergence threshold of 0.00001 and a maximum of 10,000 background points, with no test sample or bias file (Phillips, Anderson et al. 2006; Phillips and Dudík 2008; Elith, Phillips et al. 2011). To further enhance the model of each species, 10 bootstrap replicates were performed and summarized as an average. Models were additionally evaluated using the area under the curve (AUC) of the receiver operating characteristics (ROC) plot and standard deviation, as well as jackknife variables of greatest influence when used either in isolation or after omission. The influence of each oceanographic variable within each species model was calculated using the percent of relative importance (% contribution) within MAXENT.

Species richness and diversity

To assess species richness within the ETP, we generated a map following the regional partitioning scheme proposed by Pennington et al. (Pennington, Mahoney et al. 2006), based on oceanographic processes that regulate primary productivity. In concordance with the scheme presented by Pennington et al. (Pennington, Mahoney et al. 2006), and to avoid overlapping partitions, we grouped the Costa Rica Dome and Gulf of Papagayo. Specifically, we analyzed six coastal partitions and six oceanic partitions (Fig. 1b). We projected specimen data onto a map of the ETP using ARCGIS v.9.3.1 (ESRI, Redlands, CA, USA), and recorded whether a species was collected from within each of the 12 oceanographic partitions. A minimum of two individuals were required to consider a species present in any partition. We ranked each partition by the total number of flyingfish species it contained.

Flyingfish species diversity in the ETP was mapped using the following method: the study area was divided into a 1 decimal degree $\times$ 1 decimal degree grid and Shannon Indices of diversity were calculated within each cell using DIVA-GIS, v.5.2 (Hijmans, Guarino et al. 2005). Shannon Indices were projected onto a map of the ETP to visualize patterns of flyingfish species diversity throughout the study area.

RESULTS

Relative Species Abundance

All 11,125 individual specimens were examined and identified to flyingfish genus and species (Table 1). A total of 7 genera and 25 species were collected from the ETP study area.

The two most common genera were *Exocoetus* (3 species; n=5,423; 48.75% of all flyingfishes caught) and *Cheilopogon* (12 species; n=2,448; 22.0%). *Exocoetus monocirrhus* (n=3,578; 32.16%) and *Exocoetus volitans* (n=1,826; 16.44%) were the most common species, totaling nearly half of all collected individuals (n=5,404; 48.59%).

Maximum Entropy

MAXENT results indicated that the null hypothesis of random distribution with respect to the variables considered was consistently rejected in the models of all species (AUC values >0.969; st dev = 0.003; Table 2) (Tittensor, Baco et al. 2010). Mean sea surface temperature (*sstmean*) provided the greatest contribution to models for 11 of 12 flyingfish species analyzed (Table 2) and ranged from 19.2% to 41.7% (average of 30% for all species). Along with phosphate, salinity was second most important on average (13%) and the single most important variable for *H. marginatus* (22.9%), although *sstmean* ranked second (19.2%) in importance for the model of *H. marginatus*. Phosphate contributed 13% on average to the models of all species, while all other variables each contributed < 10% to models of abundant ETP flyingfish species (Table 2).

Comparisons between flyingfish genera revealed variability in the types of oceanographic data that contributed most to predictive distribution models within each genus. For example, the models of both *Exocoetus* species showed high contribution values for, dissolved oxygen, salinity and phosphate, while other values were much lower (Table 2; Fig. 2a,b). In contrast, models for *Fodiator* identified sea surface temperature, chlorophyll a and calcite as having strong influences on their predicted distributions (Table 2; Fig. 2c). *Parexocoetus* results did not show high contributions from chlorophyll a or calcite, but sea surface temperature and diffuse attenuation were clearly important (Table 2; Fig. 2d).

For some flyingfish genera, predictive distribution models were similar across species (e.g., *Exocoetus spp.*; Table 2; Fig. 2a, b), while others included species with contrasting patterns (e.g., *Cheilopogon spp.*, *Hirundichthys spp.*). For example, variables for *Prognichthys* species were different: *sstmean* influenced the model of *Pr. sealei* (41.7%) much more than it did for *Pr. tringa* (19.7%; Table 2), while the predicted distribution of *Pr. tringa* was more restricted to coastal waters than the model of *Pr. sealei* (Fig. 2c,d). *F. rostratus*, *P. brachypterus*, and *Cy. callopterus* had similar distributions along coastal regions (Fig. 2e, f, 3a). Similarly, striking differences were found among the three *Cheilopogon* species analyzed; in particular predictive distributions were large and widespread for *Ch. dorsomacula* and *Ch. xenopterus*, but restricted to coastal regions for *Ch. papilio* (Fig. 3b–d; Table 2). *Hirundichthys* species had different variables of greatest contribution from MaxEnt analysis (*salinity* for *H. marginatus*, and *sstmean* for *H. speculiger*; Table 2), but similar predictive distribution maps (Fig. 3e–f).

Species Richness

Species richness varied across oceanographic partitions within the ETP and was highest within the warmest partitions (Table 3) of the North Equatorial Current (n=16 species), North Equatorial Countercurrent and Gulf of Papagayo (n=14 species). The cold waters of

the South Pacific Subtropical Gyre and Peru Current each had very low species richness (n=1 species).

Species Diversity

The plot of species diversity resulting from the DIVA-GIS analysis revealed highest diversity north of the Equator (0°), from 130°W toward shore and north into the Gulf of California (Shannon indices >1.5; Fig. 4). Lower species diversity was found south of the Equator and toward the offshore boundaries of the study area (Shannon indices <0.5; Fig. 4).

DISCUSSION

Flyingfishes are found throughout tropical and subtropical regions of the world oceans, yet their habitats remain poorly characterized at regional scales. Further, no studies have attempted to define broad-scale patterns of flyingfish abundance, species richness and diversity. Here, we analyzed an exceptionally large dataset for flyingfishes, with over 11,000 specimens systematically collected throughout a vast region in the ETP over 21 years, and employed spatial analysis techniques to describe patterns of relative species abundance, richness and diversity, while identifying oceanographic variables that most correlate with the distributions of abundant species. Our study demonstrates that mean sea surface temperature is the best descriptive variable for the predictive distribution models of most flyingfish species in the ETP (11 out of 12 species analyzed). However, we found potentially important differences between the habitat models of some commonly collected species.

Flyingfish Species Abundance

Exocoetus was by far the most abundant and widely distributed genus in the ETP followed by *Cheilopogon*. These two genera were disproportionately well-represented in our dataset. This pattern in *Exocoetus* has been described, as several authors considered them “dominant middle-sized nekton” in the Atlantic (Nesterov and Grudtsev 1981; Grudtsev, Salekhova et al. 1987), and worldwide (Parin and Shakhovskoy 2000). The occurrence of few abundant and many rare species within a defined area is a generalizable trend known to ecologists (the Species Abundance Distribution; SAD), and remains consistent when applied to a variety of ecosystems and spatial scales (McGill, Etienne et al. 2007). For adult flyingfishes in the eastern Caribbean, Oxenford et al. (Oxenford, Mahon et al. 1995) demonstrated high relative abundance of two species (52% *Pa. hillianus* and 47% *H. affinis*) and low abundance of *Cy. cyanopterus* (~1%). In the much larger ETP study area investigated here, flyingfishes follow the SAD pattern, with few abundant species and numerous rare species. The exact mechanisms that determine SADs are not universal, but some correlations to this pattern have been observed, and may be relevant to ETP flyingfishes. For example, some authors have suggested that abundant species may have smaller body sizes (White, Ernest et al. 2007), which is the case for *Exocoetus* (among the smallest of flyingfish species: max SL = 207 mm; (Parin and Shakhovskoy 2000)). Nevertheless, other authors noted that evolutionary history may be related to the abundances of species (Cadotte, Jonathan Davies et al. 2010), and interestingly, the disproportionally abundant *Exocoetus* is one of the earliest diverging flyingfish genera (Lewallen, Pitman et al. 2011).

Predictive Distribution Models for ETP Flyingfishes

Mean sea surface temperature was most important for predictive distribution models in 11 of the 12 most abundant flyingfish species in the ETP. For marine fishes, water temperature can directly influence ontogenetic development (Watanabe and Yatsu 2004; Zwolinski, Emmett et al. 2011), spawning (Weber and McClatchie 2010), and behavior (Block, Dewar et al. 2001). Therefore, it is reasonable that this environmental characteristic may define fish habitats. For flyingfishes, gliding behavior may be energetically limited by water temperature, such that fast swimming speeds (10 m/s necessary for takeoff) are only achieved at temperatures above 20°C (Davenport 1994). However, the exact relationship between temperature and gliding behavior has not been experimentally quantified. Our data suggest that changes to sea surface temperature, both short and long-term, would have dramatic effects on the habitat boundaries and survival of many flyingfishes in the ETP.

Salinity had a high contribution (nearly 20%) in the models of four species (*E. monocirrhus*, *E. volitans*, *H. marginatus*, *H. speculiger*), suggesting that physiological constraints may limit the occurrence of some flyingfishes, although empirical evidence for such relationships are lacking. Also plausible are components of flyingfish ecology and/or water mass movements that may be directly correlated to the physical oceanography of the region. Indirect influences of flyingfish habitat need to be investigated in greater detail through experimental manipulations directed at determining physiological tolerance thresholds for each species. For example, *phosphate* was an important variable for the models of *Ch. dorsomacula*, *Ch. xenopterus*, and *E. monocirrhus*, but without necessary data on the potential effect of this nutrient on flyingfish species survival, this result is difficult to interpret.

Ph was notably lacking in contribution to ETP flyingfish species models (>2% on average), suggesting that ocean acidification may be a lesser threat to ETP flyingfish persistence than changes to sea surface temperature. Notwithstanding, MAXENT analyses resulted in predictive models for the distribution of 12 abundant flyingfish species in the ETP that may correlate with pronounced biological diversity among flyingfishes, including: egg types (e.g., buoyant, demersal, filamentous, smooth), larval morphology (e.g., single or multiple chin barbels, or no barbels), jaw morphology, spawning mode (e.g., aggregation behaviors), and two- vs. four-wing gliding strategies (Parin 1961; Collette, McGowen et al. 1984).

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Flyingfish Species Richness in the ETP

Flyingfish species richness was highest in ETP partitions with relatively higher average sea surface temperatures. For example, the warm North Equatorial Current had the highest number of observed species, while only a single species was collected in each of the coldest oceanographic partitions (South Pacific Subtropical Gyre and Peru Current). In comparison to other oceanographic partitions within the ETP, the North Equatorial Current has low primary productivity, and high sea surface temperature (Pennington, Mahoney et al. 2006). Conversely, the Peru Current is known as a primary productivity hotspot (Gutiérrez, Bouloubassi et al. 2011). Marine productivity hotspots are defined as regions of elevated chlorophyll and low SSTs that result from the upwelling of deep, nutrient-rich waters

(Valavanis, Kapantagakis et al. 2004). These ‘productivity hotspots’ are usually not correlated with increased species richness; on the contrary, they are dominated by few species with high abundance (Smith, Brown et al. 2011). Upwelling regions such as the California Current, Peru Current, and Benguela Current, are known to support some of the largest single-species fisheries in the world (Smith, Brown et al. 2011). Our results for ETP flyingfishes are consistent with this trend, suggesting that primary productivity (chlorophyll a measurements) is not a good predictor of high flyingfish species diversity.

For marine organisms, a “kinetic energy” hypothesis was proposed to explain heterogeneous patterns of species richness at a global scale (Tittensor, Mora et al. 2010). Because metabolic rates increase with temperature, it is expected that speciation rates, diversity and thermal tolerance should lead to higher species richness in warmer regions (Rohde 1992; Currie, Mittelbach et al. 2004; Clarke and Gaston 2006). Our results for ETP flyingfishes are consistent with this hypothesis. Other researchers have proposed that variance in sea surface temperature can be used to quantify the relative stability of a marine region and test the ‘climate stability hypothesis’, which predicts that stable climates have more species (Fraser and Currie 1996). Our results do not support this hypothesis because dynamic (i.e. ‘unstable’) coastal partitions (e.g. Gulf of Papagayo and Gulf of Panama; (Pennington, Mahoney et al. 2006)) have relatively high flyingfish species richness. A lack of dissolved oxygen has further been proposed as a mechanism that limits species richness (termed the ‘stress hypothesis’; (Keeling, Körtzinger et al. 2010)). For ETP flyingfishes, species richness was lower in regions characterized by higher concentrations of dissolved oxygen (e.g., Peru Current), contradicting this hypothesis. Dissolved oxygen also provided moderate contributions to models of predicted species distributions (average values of approximately 8%; Table 2).

Flyingfish Species Diversity in the ETP

We found high species diversity near shore in the ETP study area. Despite the relatively small sizes of the coastal partitions Gulf of Papagayo and Gulf of Panama, these had nearly as many observed species as the much larger North Equatorial Current and South Equatorial Current partitions (Table 3). This result was surprising, given that many flyingfishes are offshore specialists. However, the continental shelf is narrow in the ETP (Fiedler and Lavín 2006) meaning that offshore species are often found closer to shore; thus coastal partitions may capture the species diversity of both coastal and epipelagic communities. This hypothesis should be tested by comparing species diversity in regions with more extensive continental shelves, or by analyzing geographic partitions at finer scales.

CONCLUSION

This study revealed that *Exocoetus*, *Cheilopogon* and *Hirundichthys* are the most abundant genera within the ETP. After modeling the predictive distributions of the 12 most abundant species (out of 25 total), we found differences in both inter- and intra-generic comparisons, which may reflect the unique biological characteristics of each species. Mean sea surface temperature was an important predictor of flyingfish habitats in the ETP, with high contributions to the models of nearly all abundant species. Species richness measures were

higher in oceanographic features that are typically warmer, confirming that sea surface temperature is an important predictor of flyingfish abundance as well as distribution.

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Appendix 1

A summary of research cruises involved in the collection of flyingfish specimens used in this study. Research cruise names, cruise dates, ships, and chief scientists are listed.

Research Cruise Name	Cruise Date	Ship	Chief Scientist
Monitoring of Porpoise Stocks	29July1986 – 5December1986	McArthur	Dr. Rennie Holt
Monitoring of Porpoise Stocks	29July1986 – 5December1986	David Starr Jordan	Dr. Rennie Holt
Monitoring of Porpoise Stocks	30July1987 – 10December1987	McArthur	Dr. Rennie Holt
Monitoring of Porpoise Stocks	30July1987 – 10December1987	David Starr Jordan	Dr. Rennie Holt
Monitoring of Porpoise Stocks	28July1988 – 6December1988	McArthur	Dr. Rennie Holt
Monitoring of Porpoise Stocks	28July1988 – 6December1988	David Starr Jordan	Dr. Rennie Holt
Monitoring of Porpoise Stocks	28July1989 – 7December1989	McArthur	Dr. Tim Gerrodette
Monitoring of Porpoise Stocks	28July1989 – 7December1989	David Starr Jordan	Dr. Tim Gerrodette
Monitoring of Porpoise Stocks	28July1990 – 6December1990	McArthur	Dr. Tim Gerrodette
Monitoring of Porpoise Stocks	28July1990 – 6December1990	David Starr Jordan	Dr. Tim Gerrodette
Population of Delphinus Stocks	28July1992 – 2November1992	McArthur	Dr. Tim Gerrodette
Population of Delphinus Stocks	28July1992 – 2November1992	David Starr Jordan	Dr. Tim Gerrodette
Dolphin-Tuna Tracking Study	6November1992 – 5December1992	McArthur	Dr. Michael Scott
Population of Delphinus Stocks	28July1993 – 5December1993	McArthur	Dr. Tim Gerrodette
Population of Delphinus Stocks	28July1993 – 5December1993	David Starr Jordan	Dr. Tim Gerrodette
Dolphin-Tuna Tracking Study	6November1993 – 5December1993	McArthur	Dr. Michael Scott
Cetacean Acoustic Detection and Dive Interval Studies	6September1995 – 8November1995	McArthur	Dr. Jay Barlow
Vaquita Abundance Survey	4August1997 – 19September1997	David Starr Jordan	Dr. Tim Gerrodette
Vaquita Abundance Survey	4August1997 – 19September1997	Buque de Investigacion Pesqueria XI	Dr. Tim Gerrodette

Research Cruise Name	Cruise Date	Ship	Chief Scientist
Stenella Abundance Research	30July1998 – 9December1998	McArthur	Dr. Tim Gerrodette
Stenella Abundance Research	30July1998 – 9December1998	David Starr Jordan	Dr. Tim Gerrodette
Stenella Abundance Research	30July1998 – 9December1998	Endeavor	Dr. Tim Gerrodette
Stenella Abundance Research	28July1999 – 9December1999	McArthur	Dr. Lisa Ballance
Stenella Abundance Research	28July1999 – 9December1999	David Starr Jordan	Dr. Lisa Ballance
Stenella Abundance Research	28July2000 – 9December2000	McArthur	Dr. Lisa Ballance
Stenella Abundance Research	28July2000 – 9December2000	David Starr Jordan	Dr. Lisa Ballance
Chase Encirclement Stress Studies	8August2001 – 4October2001	McArthur	Dr. Karin Forney
Stenella Abundance Research	29July2003 – 9December2003	McArthur II	Dr. Lisa Ballance
Stenella Abundance Research	29July2003 – 9December2003	David Starr Jordan	Dr. Lisa Ballance
Stenella Abundance Research	28July2006 – 6December2006	McArthur II	Dr. Lisa Ballance
Stenella Abundance Research	28July2006 – 6December2006	David Starr Jordan	Dr. Lisa Ballance
Stenella Abundance Research - Line Transect and Ecosystem Survey	18August2007 – 29November2007	McArthur II	Dr. Eric Archer

Fig. 1.

a. Flyingfish specimen collection localities from research cruises in the eastern tropical Pacific study area from 1986 – 2007. Black dots represent dipnet stations, and the gray polygon is an outline of the study area. **b.** Map of the 12 oceanographic partitions within the eastern tropical Pacific study area drawn using ARCGIS, version 9.3.1 (ESRI, Redlands, CA, USA) and the descriptions from (Pennington, Mahoney et al. 2006). 6 oceanic partitions (NEC = North Equatorial Current, CCTR = Countercurrent Thermocline Ridge, NECC = North Equatorial Countercurrent, EU = Equatorial Upwelling, SEC = South Equatorial Current, SPSG = South Pacific Subtropical Gyre) and 6 coastal partitions (CC = California Current, TEH = Gulf of Tehuantepec, PAP = Gulf of Papagayo, PAN = Gulf of Panama, GAL = Galapagos, PC = Peru Current) were included.

Fig. 2. Predicted species distribution models for six abundant flyingfish species collected in the ETP study area, based on MAXENT analyses: **a.** *Exocoetus monocirrhus*, **b.** *Exocoetus volitans*, **c.** *Prognichthys sealei*, **d.** *Prognichthys tringa*, **e.** *Fodiator rostratus*, **f.** *Parexocoetus brachypterus*. Shaded areas correspond to regions of highest probability of occurrence as determined by average consensus after 10 bootstrap replicates for each species (Warmer colors = higher probability of occurrence).

Fig. 3. Predicted species distribution models for six abundant flyingfish species collected in the ETP study area, based on MAXENT analysis results **a.** *Cypselurus callopterus*, **b.** *Cheilopogon papilio*, **c.** *Cheilopogon dorsomacula*, **d.** *Cheilopogon xenopterus*, **e.** *Hirundichthys marginatus*, **f.** *Hirundichthys speculiger*. Shaded areas correspond to regions of highest probability of occurrence as determined by average consensus after 10 bootstrap replicates for each species (Warmer colors = highest probability of occurrence)

Fig. 4.

A projected interpolation of results from species diversity estimates (measured using the Shannon Index within DIVA-GIS v.5.2; (Hijmans, Guarino et al. 2005). Light pink colors represent cells with lowest species diversity, and dark pink colors represent cells with highest species diversity. The gray polygon outlines the eastern tropical Pacific study area.

Table 1

Numbers of flyingfish genera and species collected within the ETP study area. The total collection number of each genus and species is listed. Percent abundance and rank order abundance estimates were calculated for each species.

Genus	n	%	Rank	Species	n	%	Rank
<i>Exocoetus</i>	5423	48.75	1	<i>Exocoetus monocirrhus</i>	3578	32.15	1
<i>Cheilopogon</i>	2398	21.56	2	<i>Exocoetus volitans</i>	1826	16.44	2
<i>Hirundichthys</i>	1403	12.61	3	<i>Cheilopogon xenopterus</i>	1224	11.00	3
<i>Prognichthys</i>	1090	9.80	4	<i>Prognichthys tringa</i>	963	8.65	4
<i>Fodiator</i>	473	4.25	5	<i>Hirundichthys marginatus</i>	846	7.60	5
<i>Cypselurus</i>	242	2.18	6	<i>Cheilopogon papilio</i>	554	4.98	6
<i>Parexocoetus</i>	96	0.86	7	<i>Hirundichthys speculiger</i>	530	4.76	7
Total	11125			<i>Fodiator rostratus</i>	473	4.25	8
				<i>Cheilopogon dorsomacula</i>	427	3.84	9
				<i>Cypselurus callopterus</i>	192	1.73	10
				<i>Prognichthys sealei</i>	127	1.14	11
				<i>Parexocoetus brachypterus</i>	96	0.86	12
				<i>Cheilopogon furcatus</i>	91	0.82	13
				<i>Cypselurus angusticeps</i>	50	0.45	14
				<i>Cheilopogon spilonotopterus</i>	33	0.30	15
				<i>Cheilopogon pinnatibarbatus</i>	30	0.27	16
				<i>Cheilopogon hubbsi</i>	25	0.22	17
				<i>Exocoetus peruvianus</i>	19	0.17	18
				<i>Hirundichthys albimaculatus</i>	15	0.13	19
				<i>Hirundichthys rondeletii</i>	12	0.11	20
				<i>Cheilopogon atrisignis</i>	5	0.04	21
				<i>Cheilopogon rapanouiensis</i>	3	0.03	22
				<i>Cheilopogon arcticeps</i>	3	0.03	23
				<i>Cheilopogon unicolor</i>	2	0.02	24
				<i>Cheilopogon abei</i>	1	0.01	25

Table 2

A summary of MAXENT analysis results for each of the most abundant species (12 species; n = 96). Abbreviated variable names, genera, and species are listed in columns. A grayscale heat map in the main frame of the table highlights percent contributions of the most influential variables for each species model. Also calculated are the total percent contributions and averages for each variable across all species. Model summaries include area under the curve (AUC) values and standard deviation, the name of each variable that had the highest contribution percentage, jackknife variables that contributed the most to each model when used in isolation or after omission.

	Cheilopogon				Cypselurus		Exocoetus		Fodiator		Hirundichthys		Parexocoetus		Prognichthys		All Models		
	dorsomacula	papilio	xenopterus	callopterus	monocirrhus	volitans	rostratus	marginatus	speculiger	brachypterus	scaei	tringa	Total	Average					
Greatest contribution	sstmean	28.3	31.8	26.5	38.2	25.3	26.9	32.8	19.2	29.9	35	41.7	19.7	355	30				
	salinity	14.8	3.9	16	7.6	19.6	16.8	4.5	22.9	26.5	9.9	11.1	7.5	161	13				
	phosphate	19	10.7	18.2	7	21.1	17.4	7.2	16.2	11.9	7.8	3	14.8	154	13				
	damean	7	6.8	7.1	15.8	6.1	1.4	0.7	2.8	2	22.6	10.1	11.8	94	8				
	dissox	15.5	0.7	16.8	0.4	18.9	11.6	0.3	7.5	8.9	6	0.1	6.1	93	8				
	nitrate	3.5	5.8	4.3	10.2	3.3	9.8	4.5	2.3	7.5	0.8	12.1	18.8	83	7				
	calcite	7.1	10.7	1.8	12	0.8	1.4	15.8	0.4	0.3	7.4	12.9	9.1	80	7				
	chlomean	2	15	3.9	2.3	1.9	4	29.9	5	1.9	2.8	0.1	3	72	6				
	parmean	2	4.2	1.7	0.4	1.1	7.2	1.1	13.4	2.4	0.6	1.2	7.3	43	4				
	silicate	0.1	3.9	2.4	1.9	1.7	3	0.6	10	8.5	0	6.3	0.7	39	3				
Jackknife (isolation)	ph	0.5	6.4	1.1	3	0.3	0.5	2.5	0.3	0.1	6.9	1.6	1.1	24	2				
	AUC	0.984	0.995	0.978	0.995	0.969	0.976	0.997	0.985	0.985	0.996	0.994	0.991						
	St. dev.	0.001	0.001	0.001	0.000	0.001	0.001	0.001	0.001	0.001	0.003	0.000	0.000						
Jackknife (omission)	Greatest contribution	sstmean	sstmean	sstmean	sstmean	sstmean	sstmean	sstmean	salinity	sstmean	sstmean	sstmean	sstmean	sstmean	sstmean	sstmean	parmean	nitrate	
	Jackknife (isolation)	dissox	parmean	dissox	sstmean	dissox	dissox	chlomean	dissox	sstmean	sstmean	sstmean	parmean	sstmean	sstmean	sstmean	parmean	nitrate	
Jackknife (omission)	Jackknife (omission)	salinity	parmean	salinity	nitrate	salinity	salinity	sstmean	salinity	damean	nitrate	nitrate	nitrate						

Table 3

Species richness counts within each of the 12 oceanographic partitions sampled in this study. A minimum of two specimens was required for a species to be considered present in a partition.

Name of Oceanographic Partition	<i>n</i>
North Equatorial Current (NEC)	16
North Equatorial Countercurrent (NECC)	14
Gulf of Papagayo (PAP)	14
Gulf of Panama (PAN)	13
California Current (CC)	12
Countercurrent Thermocline Ridge (CCTR)	10
South Equatorial Current (SEC)	10
Gulf of Tehuantepec (TEH)	10
Equatorial Upwelling (EU)	8
Galapagos (GAL)	3
South Pacific Subtropical Gyre (SPSG)	1
Peru Current (PC)	1