# META-ANALYSIS OF REEF FISH DATA IN HAWAII: BIOGEOGRAPHY AND GRADIENTS OF HUMAN IMPACTS

*Final Report to DAR, Fall 2013*


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## *Executive Summary*

- **One of the major obstacles to wise management of coral reef fisheries is the lack of sound information** on population abundance at spatial scales commensurate with the uses of these resources. This information is critical to developing sustainable fisheries management strategies, improving management of existing Marine Protected Areas (MPAs), designing future MPA networks, and aiding in the development of comprehensive marine spatial planning.

- There are currently a number of disparate data sets for reef fishes from around the Hawaiian Islands but no single data set is spatially comprehensive enough to explain the natural and anthropogenic processes that affect the distribution, abundance, and size of reef fishes around the state. **This study, for the first time, has synthesized all these data sets into a single and spatially comprehensive database** in order to characterize reef fish assemblages around Hawaii while controlling for habitat, wave exposure, and geographic influences.

- We compiled **25 datasets, representing more than 25,000 individual fish surveys** from throughout the entire Hawaiian Archipelago since the year 2000. These data were rigorously checked for errors and integrated into a common database with a standardized structure.

- **Information on fish species life history and ecology** (e.g., length-weight parameters, trophic position, movement, feeding ecology) are imperative to the assessment of fish populations. We used this opportunity to compile all known information on these fishes so that a **standardized database is now available** for the scientific community.

- Length-weight relationships of reef fishes were compared over time and space. Overall the relationship across all species did not change over time, however **on average fishes in the** Northwestern Hawaiian Islands **(NWHI) were heavier for a given length than in the** main Hawaiian Islands **(MHI)**.

- We developed **the first ever bioregionalization of the Hawaiian Archipelago** based on abundance and biomass of reef fishes. Results show clear separation between the MHI and NWHI but also a number of additional faunal breaks driven primarily by the relative abundance of **endemic species**.

- **Endemic species were much more common at the northern end of the chain** and showed a strong and statistically significant negative correlation with latitude. Endemics made up 52-55% of the numerical abundance at the northern end of the archipelago but only 17% on Hawaii Island in the extreme south.

- We conducted unconventional assessments for 52 species within the MHI by comparing their abundance to the NWHI (Papahānaumokuākea Marine National Monument-PMNM)—a large (362,073 km-2), virtually unfished reference area. **This preliminary assessment has identified a number of species that require immediate management action. Over one-quarter of the species (27%) examined in the MHI appeared to be depleted below 10% of unfished abundance, while 42% were below 25% of unfished abundance.**

- The traditional Hawaiian district or **moku was used as a unit of spatial stratification**. **Moku explained 63% of the variability in resource fish biomass** and explained much of the variability in many other fish assemblage metrics. We attributed a number of biological, physical, and human demographic information to each moku for analytical purposes.

- **Biomass of resource species was negatively correlated with human population pressure among mokus**. We used human population per moku divided by shoreline length for that moku as an index of human population pressure. There was a strong negative relationship between resource fish biomass and human population pressure showing that biomass was extremely low in areas with high human population pressure and even modest human population pressure had a negative impact on fish assemblage structure. However, a number of remote areas with low human populations maintain high standing stock of fishes and these areas are likely important refugia for maintaining fisheries production and biodiversity functioning in the MHI.

- **Resource fish biomass was highest in mokus with northern and easterly exposures.** Mokus with southern and westerly exposures have less severe sea conditions resulting in greater accessibility and therefore heavier fishing pressure in these locations.

- **MMAs around the populated areas of Oahu and Maui showed higher biomass relative to fished areas. However, overall biomass within these protected areas was lower than MMAs on Hawaii Island and Lanai, where overall human pressure is lower.**

- **Ahihi-Kinau Natural Area Reserve on Maui was the most effective fully protected MMA** when MMA size is considered in calculating total resource fish biomass.

- **Older MMAs had the highest resource fish biomass while newer MPAs had fewer numbers and smaller sizes of resource fishes.**

Overall, this synthesis is the first ever, comprehensive examination of reef fish assemblage structure across Hawaii. The results show clear, distinct bioregions across the archipelago that give us a better understanding of reef fish macroecology and have important implications for management at the regional scale. The findings from this study also highlight the negative impacts of human population pressure on reef fishes, particularly around Oahu and Maui. When compared with the NWHI, a large proportion (42%) of MHI reef fish stocks were below 25% of unfished abundance. However, there are still remote areas in the MHI that provide refugia and help sustain fish stocks, therefore these areas are important conservation hotspots. MMAs were shown to be effective in conserving fishes, especially around Oahu and Maui where fishing pressure is extremely high outside of MMAs. However, most of these areas are too small to have substantial fisheries benefits. As a result, a more holistic approach that includes community-based management, expansion of the MMA network with a greater emphasis on no-take reserves, improvements to current fisheries regulations including enhanced enforcement efforts, and finally a greater emphasis on marine education and ocean awareness are necessary.

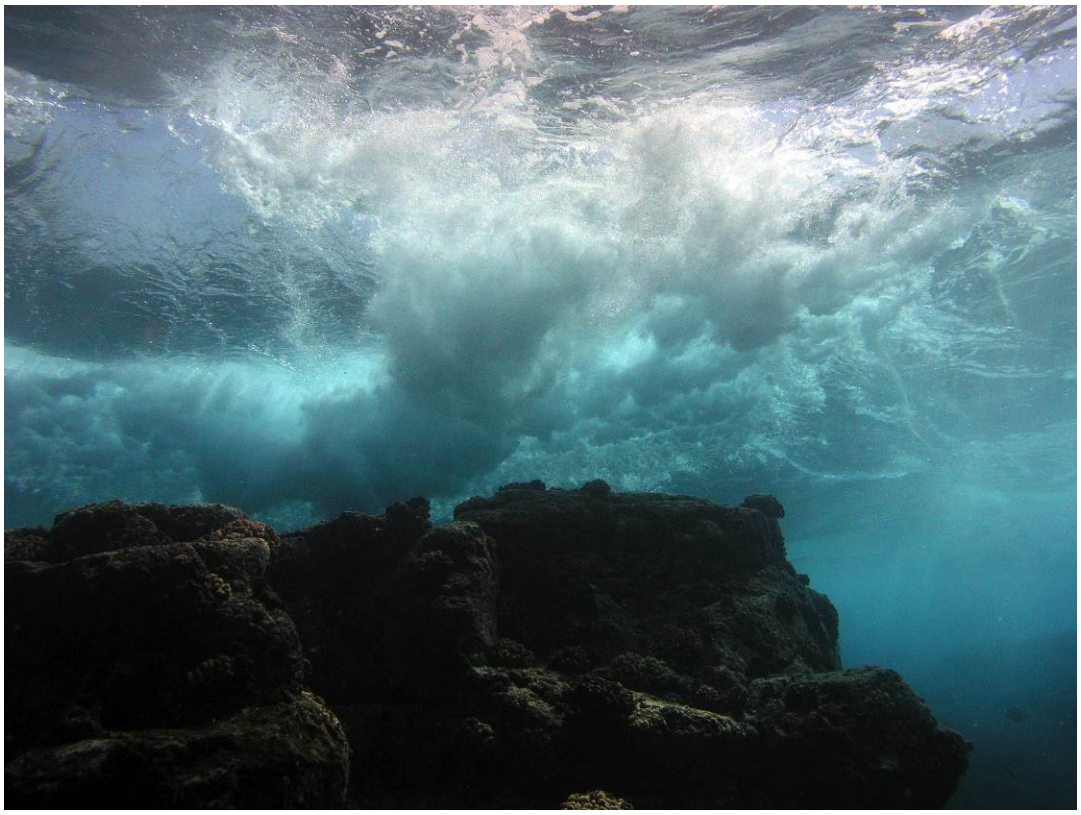


Photo: K.Stamoulis

## *Introduction and Background*

Overfishing is thought to be one of the major reasons for the decline in coral reef resources across Hawaii and elsewhere (Friedlander and DeMartini 2002, Williams et al. 2008). These declines are also associated with, land-based pollution, destruction of habitat, invasive species and other threats, which are driven at the underlying level by a growing human population, export-driven markets for resources, access to technological innovations (e.g., motorized boats and freezers for storing catch), introduction of new and overly efficient fishing techniques (e.g. inexpensive monofilament gill nets, SCUBA, GPS), and loss of traditional conservation practices (Friedlander et al. 2003, 2008, 2013). Further, there is poor compliance with state fishing laws and regulations and insufficient enforcement, which are partially attributed to lack of resources and capacity.

Hawaii's coral reef fisheries provide livelihoods, sustenance, recreation, and help to perpetuate cultural practices in the Hawaiian Islands. One of the major obstacles to wise management of coral reef fisheries resources is the lack of good information on population abundance at spatial scales commensurate with the uses of these resources. Although many people acknowledge declines in certain reef fishes in Hawaii over time, there is little agreement on the causes of these declines.

There are currently a number of disparate data sets for reef fishes around the Hawaiian Islands but no single data set is spatially comprehensive enough to understand the natural and anthropogenic processes that affect the distribution, abundance, and size of reef fishes around the state. This information is critical to developing sustainable fisheries management strategies, improving management of existing MMAs, helping to design future MMA networks, and aiding in the development of comprehensive marine spatial planning.

This study describes population structure of reef fishes across the entire archipelago and therefore helps to elucidate the spatial patterns of abundance that are useful for informing management and marine spatial planning. This study, for the first time, compiles all known existing reef fish visual census data from Hawaii into a single dataset. Additionally, we have attributed all species within the database with information on life history and functional traits.

This study synthesizes this information into three major topics:

I. Spatial and temporal comparison of length-weight relationships
II. Bio-regionalization of Hawaiian fish fauna
III. Fish assemblage structure across a gradient of human impact

*Regional database of species life history*

Information on fish species life history and ecology are imperative to the assessment of fish populations. This includes information such as length-weight parameters, trophic position, and feeding ecology. Length-weight parameters are used to calculate biomass from underwater visual census where size and counts of fishes are recorded. Numerous researchers in the state of Hawaii use these data on a regular basis, yet a standardized fish species database does not yet exist. We used this opportunity to bring together all known information on these fishes by combining species data from contributors and will publish this information so that a standardized database will be available for future efforts among the entire research community (Appendix 1). This will greatly increase uniformity as research moves forward.

*Regional database of fish census data*

We developed a standard template and compiled known fish census data into a comprehensive database. Data sets were identified from around the archipelago that collectively represents a variety of habitats, depths, and human influences. Nine individual researchers and managers of monitoring programs were contacted resulting in 25 datasets and over 22,000 individual surveys.

*Spatial and temporal comparison of length-weight relationships*

Length-weight relationships in fishes are central to understanding the status and condition of fish populations, and are critical for estimating biomass from length observations (Froese 2006, Pauly 1993). The first goal of this study is to publish length-weight relationships for Hawaiian fishes for the first time. Data on weight and length of reef fishes were gathered from multiple sources, including an extensive database held by the Hawaii Cooperative Fishery Research Unit at the University of Hawaii dating back to 1980 when large collections occurred in the Northwestern and Main Hawaiian Islands. Additional data were gathered from multiple sources dating back to 2002 and covering the entire archipelago. The extent of these surveys allowed for further analysis of spatial and temporal changes in fish condition.

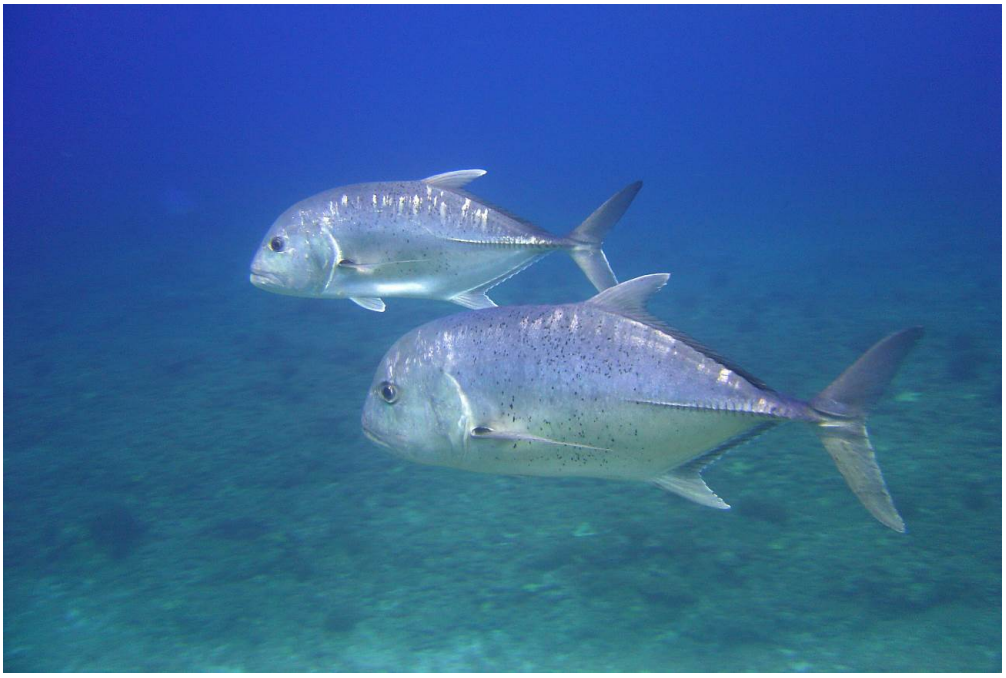
*Bio-regionalization of Hawaiian fish fauna*

Delineating regions is important in advancing our understanding of the biogeography and ecology of ecosystems, as well as understanding the historical and evolutionary forces shaping biodiversity patterns. From an applied point of view, this delineation is also very important in the identification of conservation priorities based on the composition of species assemblages. A biogeographic framework was developed to examine natural and anthropogenic factors that influence patterns of reef fish assemblage structure across one of the most

unique and isolated marine ecosystems on earth. We combined the observational data with information on each species' life history traits and known geographic distributions to develop hypotheses about spatial patterns of abundance and biomass along latitudinal, oceanographic and anthropogenic gradients. Geographic patterns were explored following a rigorous quantitative approach, with analyses covering various metrics (e.g. numerical density, biomass, trophic structure) based on concepts from biogeography theory. This work serves to identify important faunal breaks and spatial patterns of fish assemblage structure across the archipelago that will help to define regional management strategies in Hawaii and contribute to or understanding of reef fish macroecology.

*Fish assemblage structure across a gradient of human impacts*

Spatial variation in fish assemblages is evident throughout the archipelago and has been shown to correlate with human population pressure (Williams et al. 2008). We extend our understanding of the status and structure of fish assemblages across a human impact gradient by comparing metrics based on traditional Hawaiian management boundaries (mokus). This included comparisons of the relative influences of human population density and physical and anthropogenic factors on distribution, abundance, and size of reef fish around the state. We also evaluated existing MPAs based on their size and time since establishment.



Giant Trevally – ulua aukea (*Caranx ignobilis*) Northwestern Hawaiian Islands. Photo: K. Stamoulis

## *Regional database of fish census data*

Data from government and non-government sources were compiled into a single database in a consistent structure. Individual researchers and lead persons for monitoring programs were contacted to acquire data on underwater visual surveys of fish assemblages. The final database covered 25 individual datasets from 9 principal investigators. Encompassing these are 7 major data sources (Table 1).

Table 1. Summary of fish datasets compiled from government and non- government sources and used in this analysis.

| Data Source | Point of Contact | Survey Method | Total Number Surveys | Count of Islands | Years of Surveys |
|---|---|---|---|---|---|
| **CRAMP** | Kuulei Rodgers | Belt | 371 | 8 | 2000, 2001, 2002, 2012 |
| **RAMP/CRED** | Ivor Williams | Belt & SPC | 5118 | 17 | 2000-2012 |
| **DAR** | Walsh, Sparks, Schumacher | Belt | 8980 | 4 | 2004-2012 |
| **FERL** | Alan Friedlander | Belt | 662 | 3 | 1993, 1994, 1999, 2000, 2003-2007, 2010-2012 |
| **FHUS** | Alan Friedlander | Belt | 1463 | 4 | 2002-2004, 2006-2008 |
| **NPS** | Eric Brown | Belt | 501 | 2 | 2004-2012 |
| **TNC** | Erik Conklin | Belt | 814 | 4 | 2009-2012 |

Meta-data from each dataset were compiled and analyzed to identify spatial and temporal gaps in these data. One previous study has been conducted using visual census of fishes within the Main Hawaiian Islands (Williams *et al.* 2008), but these data were limited in spatial extent and habitat. In addition, large efforts to collect additional data have occurred since 2006 when this analysis was conducted. Figure 1 presents a comparison of the spatial extent of data collection in the Main Hawaiian Islands in Williams et al. 2008 and the current analyses. Large gaps in the previous dataset included the west coast of Hawaii, north coast of Molokai, south and west Kauai, south and east Oahu, and Kaho‘olawe, and are now covered by our more comprehensive dataset. Additionally, increased sampling around Ni’ihau, west Maui, and all coastlines of Oahu provide additional power to the analyses and allow us to identify general patterns among islands with greater certainty. Likewise, this study has incorporated data from the entire Hawaiian Archipelago, including 18 islands with sites spanning nearly 10° of latitude and over 2,500 km (Figure 2, Table 2).

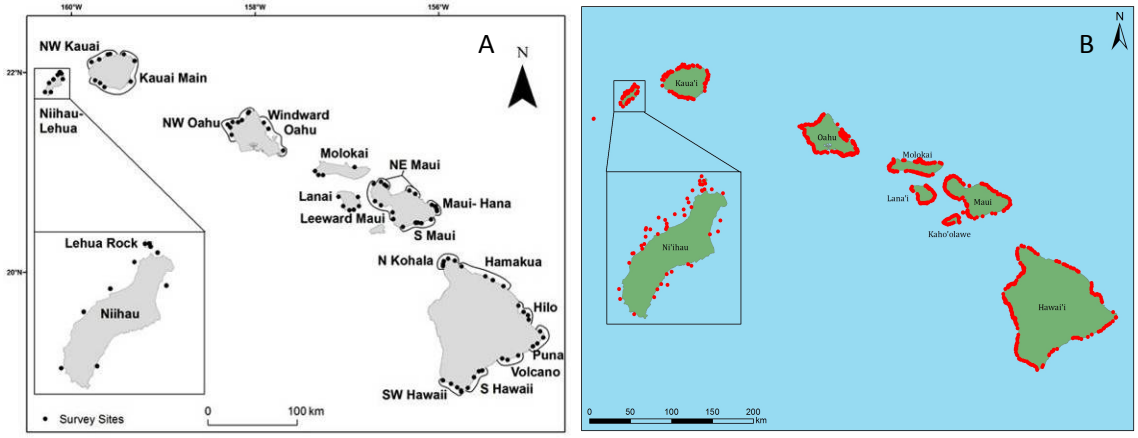



Figure 1. Comparison of spatial coverage of data points in the MHI from (A) previous analysis in Williams (2008), and (B) current study database.

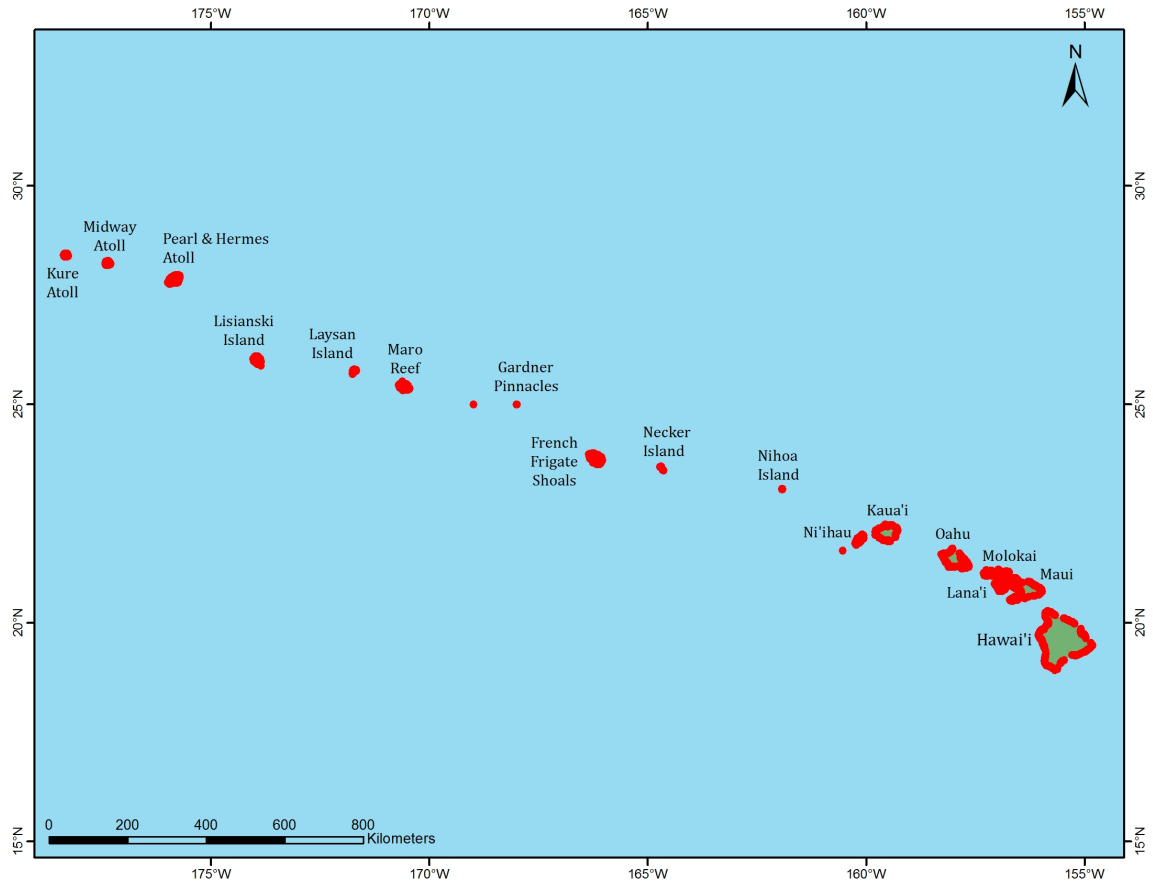



Figure 2. Individual surveys sites across the Hawaiian Archipelago.

Data collection efforts varied considerably across the islands (Figure 3, Table 2), with Hawaii Island having the largest level of effort followed by Maui and Oahu. Hawaii DAR contributed 46% of the 22,103 surveys, followed by NOAA CRED

(34%), and the Fisheries Ecology Research Lab at the University of Hawaii (FERL) (13%). Nearly 47% of the surveys were conducted around Hawaii Island, followed by 11% on Maui and Oahu. The number of surveys increased dramatically after 2003 due to increased efforts by NOAA CRED and Hawaii DAR. The efforts by NOAA CRED have been scaled back in recent years but efforts by TNC and FERL have increased (Figure 4).

Table 2. Number of surveys for each island, ordered from north to south and attributed by data source.

| **Island** | **Dataset** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **CRAMP** | **RAMP** | **DAR** | **FERL** | **FHUS** | **NPS** | **TNC** | **Total** |
| Kure | | 678 | | | | | | 678 |
| Midway | | 565 | | | | | | 565 |
| Pearl & Hermes | | 1070 | | | | | | 1070 |
| Lisianski | | 535 | | | | | | 535 |
| Laysan | | 239 | | | | | | 239 |
| Maro | | 644 | | | | | | 644 |
| Gardner | | 60 | | | | | | 60 |
| French Frigate | | 908 | | | | | | 908 |
| Necker | | 133 | | | | | | 133 |
| Nihoa | | 32 | | | | | | 32 |
| Kauai | 83 | 296 | | 192 | | | | 571 |
| Niihau | 10 | 256 | | | | | | 266 |
| Oahu | 57 | 368 | 462 | 446 | 882 | | 125 | 2340 |
| Molokai | 29 | 259 | | 24 | | 263 | | 575 |
| Maui | 98 | 508 | 1405 | | 446 | | 51 | 2508 |
| Lanai | 26 | 266 | 235 | | 73 | | | 600 |
| Kahoolawe | 8 | | | | | | 44 | 52 |
| Hawaii | 69 | 668 | 8138 | | 620 | 238 | 594 | 10327 |
| ***Grand Total*** | *380* | *7485* | *10240* | *662* | *2021* | *501* | *814* | ***22103*** |

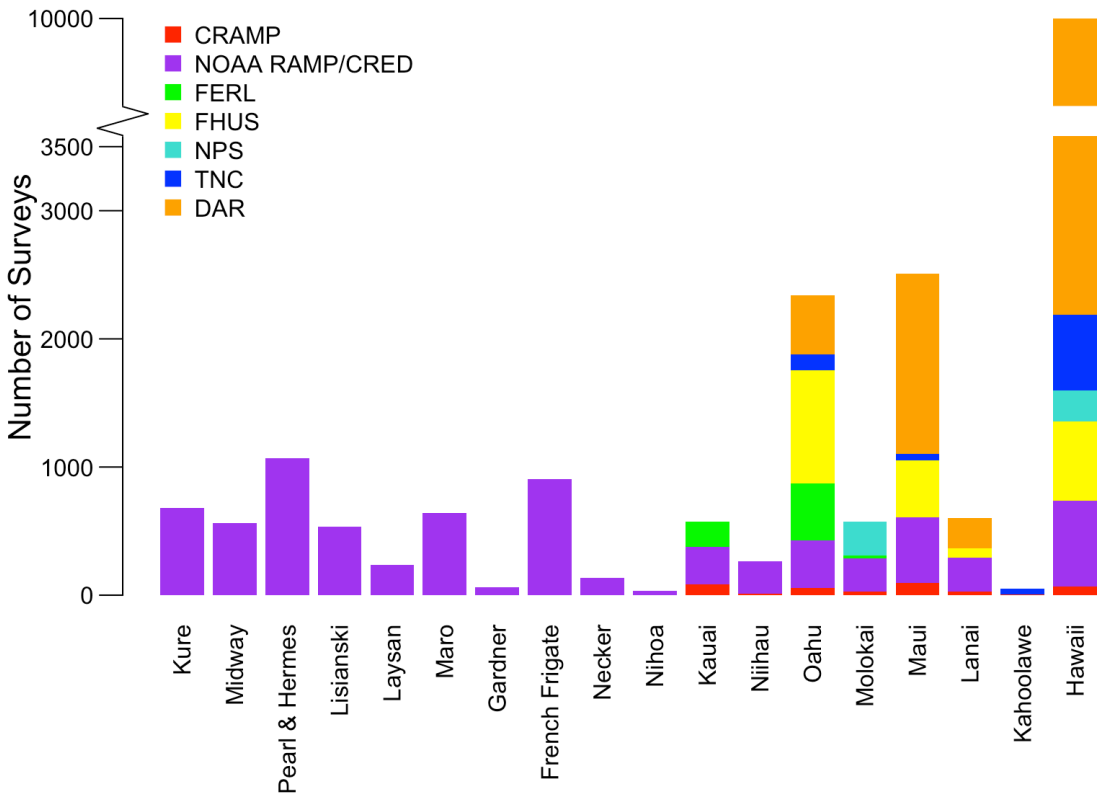



Figure 3. Number of surveys for each island, ordered from north to south and attributed by data source.

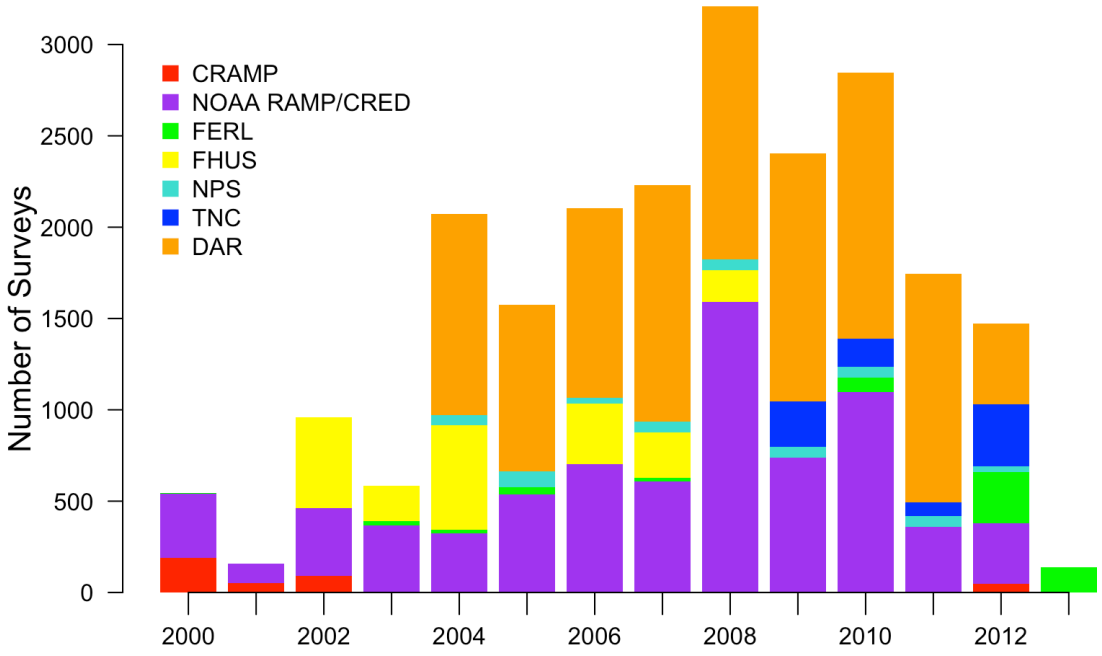



Figure 4. Number of surveys by year, attributed by data source.

## *Spatial and temporal comparison of length-weight relationships*

Length-weight relationships of fishes are central to understanding the status and condition of fish populations and critical for estimating biomass from length observations. This relationship is also among the most common model used in fisheries science (Pauly 1993). Despite their critical importance, length-weight relationships are only known for a restricted suite of species and are confined in geographic coverage. This is particularly true and important for Hawaii, which is one of the most isolated archipelagos on earth and has a high number of endemic fishes. Hawaii is also situated at the furthest extent of the tropics and can be characterized as a sub-tropical environment; therefore length-weight relationships for wide-ranging species may be different in Hawaii than in more tropical locations.

Length-weight relationships also provide a useful comparison of fish condition since weight at a given length is greater for a fish in better condition (Tesch 1968, Froese 2006). This is related to the concept of allometry, where growth follows a power law function with the slope of the regression between weight and length equal to 3 if the weight of the fish does not change as it gets longer. If the slope is different than 3 the fish exhibits allometric growth and can either become skinner or heavier as it grows (Tesch 1968). Changes in this relationship provide insight into relative differences in 'condition' between populations, or for a given population over time.

Variability in life history also has implications for fisheries management and our understanding of population dynamics. Length-weight relationships can be compared to examine the relative condition or robustness of population, both spatially and temporally. Variation in weight of fishes can occur for a variety of reasons, including density-independent and density-dependent factors.

In this study, length-weight relationships were described for 112 fish species specific to nearshore Hawaiian waters (Appendix II). Data were compiled from multiple sources, including a historic database dating back to 1979 from the Hawaii Cooperative Fishery Research Unit at the University of Hawaii. These historic data were matched with more contemporary sampling, providing a unique opportunity to compare relationships in space and time.

The goals of the project were three-fold:

a) Publish Hawaii-specific length-weight parameters for coral reef fishes, with particular focus on endemic species
b) Conduct a comparison of fish length-weight relationships between two time periods: 1979-1985 and 2002-2012, which represent different ocean productivity regimes due to changes in the Pacific Inter-decadal Oscillation (PDO)
c) Conduct a comparison of fish length-weight relationships between the Main and Northwestern Hawaiian Islands

A temporal comparison of fish length-weight relationships between the 1980s and the 2000s provides a unique opportunity to evaluate differences in a change in oceanic productivity associated with the Pacific Decadal Oscillation (PDO). Polovina *et al*. (2008) studied decadal changes in productivity boundaries in Hawaii and found two distinct decadal periods. The northern portion of the archipelago prior to 1987 was characterized by greater vertical mixing, resulting in more productive winters during this time period compared to today. This leads to the hypothesis that for a give length, fish should be heavier in the 1980s when productivity was greater. Spatial comparisons of fish length-weight relationships between the Main and Northwestern Hawaiian Islands allows for further testing of hypotheses related to biophysical gradients while controlling for time. Total abundance of fishes varies greatly between the Main and Northwestern islands and is hypothesized to be related to high fishing pressure in the populated, Main Hawaiian Islands (Friedlander & DeMartini 2002, Williams et al. 2008).

*Database*

Available data were compiled for all coral reef-associated fishes in Hawaiian waters from a wide range of data sources and time periods. The majority of these data come from the Hawaii Cooperative Fisheries Research Unit's inventories of fishes from poison stations in the NWHI and from Puako, West Hawaii in the 1980s. Additional data were compiled by contacting individual researchers and from large-scale collections of fishes in the NWHI from research cruises for genetic sampling. This was supplemented with additional information from published sources, theses, and grey literature.

The resulting database is comprised of 17,354 individual observations of fishes from 282 species. Of those, 196 species had >10 observations. Data were quality controlled and corrected by careful evaluation of each data point. Outliers and suspicious data points were removed from analysis on the basis of assumed misidentification, incorrect units, and other data entry errors. This resulted in another 84 species without adequate information or that did not conform to assumptions of the linear models. A final list of 109 species with adequate information and data were used to conduct length-weight analysis (Appendix II).

Length measurements were provided as standard length (SL), fork length (FL) or total length (TL). All measurements were converted to TL using relationships between SL/FL and TL established from the database and from known sources via FISHBASE (Froese and Pauly 2013).

*Model*

The allometric equation for weight at length was provided by Keys (1928) and further refined by Le Cren (1951) in the form:

$$W = aL^b$$

where *W* is weight in grams, *L* is length in cm, and *a* and *b* are fitting parameters. The equation is commonly calculated in logarithmic form as:

$$\log W = \log a + b \log L$$

Models were fit to the log-form with standard least-squares regression for each species individually and for the groups of species combined. Fitted parameters were back-transformed with a bias-correction factor that included an adjustment for the transformation bias. This is necessary since back-transformation from a log-scale underestimates the mean value on the original scale since the log-scale mean is equal to the geometric mean. The bias-correction factor took the form:

$$e^{\sigma^2/2}$$

*Temporal Comparison*

Fish condition can be explained by the fitting parameter *b* from the allometric equation defined above which describes the slope of the curve. Fishes with a slope greater than 3 exhibit positive allometric growth, meaning an individual weighs more for a given length. Overall, the relationship between length and weight for 21 species of fishes did not change significantly over time, however comparisons suggest that many species were heavier for a given length in the 1980s compared to more recently. Fishes collected between 1979 and 1985 had slopes ranging from 2.8-3.5, whereas collections for the same species from 2002-2012 had slopes ranging from 2.3-3.3 with the tail of the distribution skewed towards smaller numbers in the more recent data (Figure 5). The mean slopes were not significantly different between time periods (*t*=1.5, df= 37.8, *p*=0.14). Overall, species exhibited more positive allometric growth in the earlier time period with the mean value greater than 3 (*t*=1.9, df= 20, *p*=0.07).

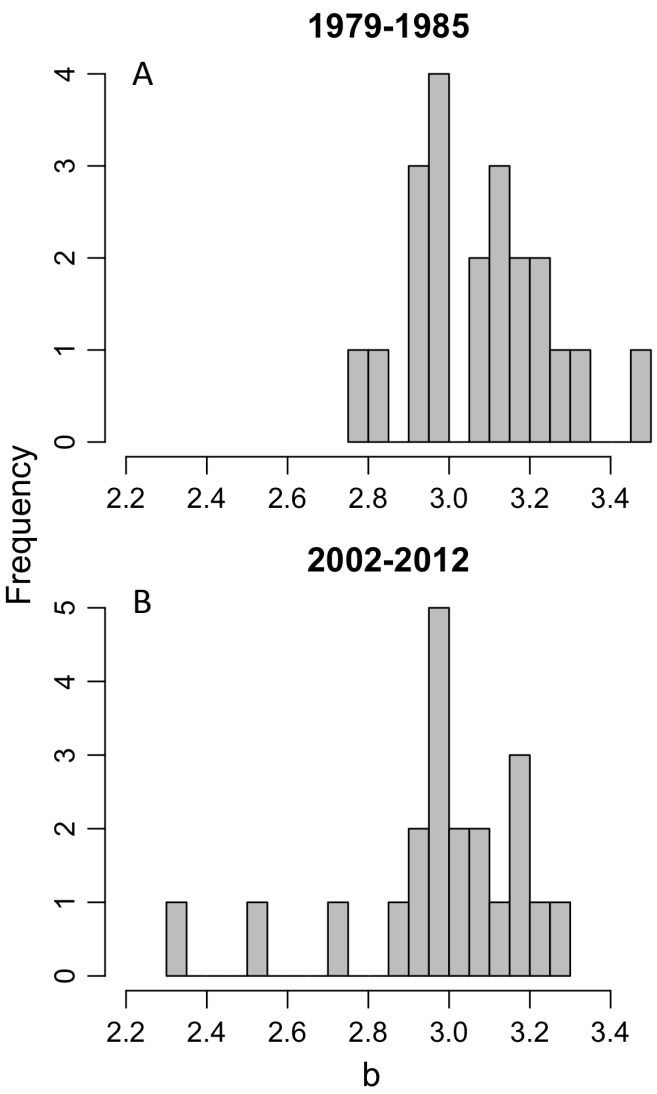



Figure 5. Distribution of values for slope of length-weight regression for 21 species in two time periods

Comparing the slope of the length-weight regression for individual species provides information about the direction of change in individual species condition across changes in the inter-decadal oscillation. There were a greater number of species with slopes less than 3 in 2002-2012 (n=9) than in the earlier, more productive time period (Figure 6). Those species with a greater slope in the more recent time period (2002-2012) were different from our prediction that the greater productivity during the last decadal oscillation would result in better conditions for fish growth.

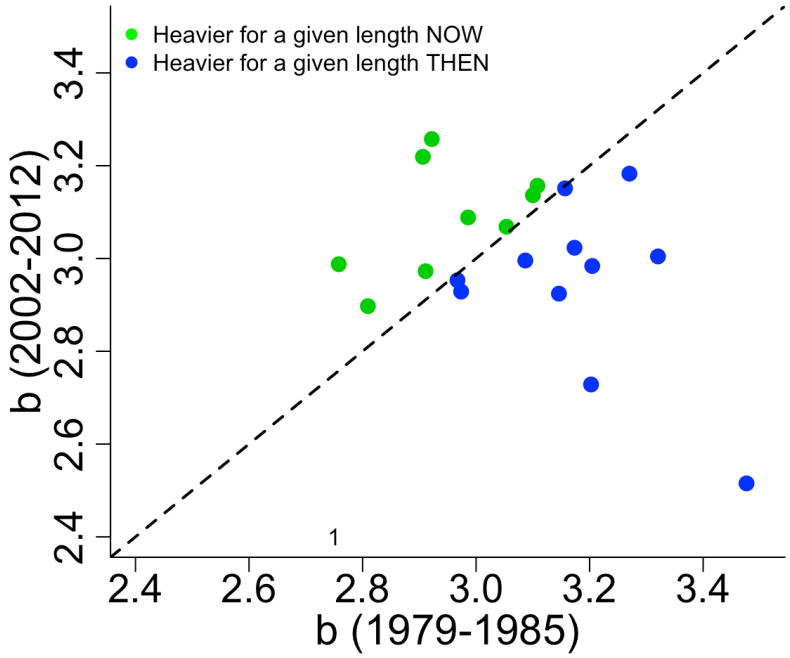



Figure 6. Comparison between slopes for each species in 1979-1985 and 2002-2012. Points above the line represent species with a greater slope in the more recent time period (green) and points below the line represent species with a greater slope in the earlier time period (blue).

*Spatial Comparison*

Comparisons of length-weight relationships between the Main Hawaiian Islands and the Northwestern Hawaiian Islands were restricted to the most recent time frame to avoid confounding results of space and time. In general, the NWHI experiences a different oceanographic regime than the MHI with colder winters and warmer summers with greater productivity. This leads to the hypothesis that fishes in the NWHI will be larger for a given length compared with the MHI.

Length-weight relationships were compared for 23 species between the NWHI and MHI. The slope of the length-weight relationship was significantly higher in the NWHI compared to the MHI ($t$=-2.23, df= 33.14, $p$=0.03; Figure 7). Slopes in the MHI did not differ significantly from 3 ($t$=0.16, df= 22, $p$=0.87; Figure 7a). Conversely, slopes in the NWHI were, on average, significantly greater than 3,

and therefore fishes tended to be heavier as length increased ($t$=-2.60, df= 22, $p$=0.02; Figure 7b)

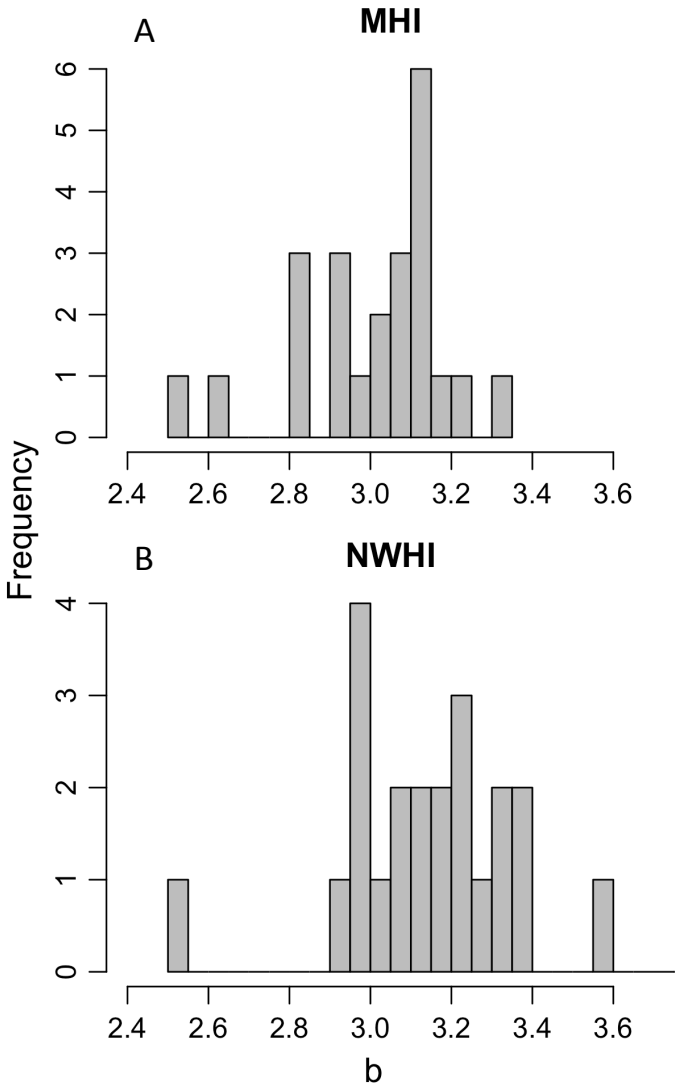



Figure 7. Distribution of values for slope of length-weight regression for 23 species in the MHI and NWHI

Within individual species, the slope of the length-weight regression provides information about the direction of change in individual species' condition between the MHI and NWHI. Sixteen species had a greater slope in the NWHI then the MHI compared to only 7 with the opposite pattern (Figure 8). Interestingly, 5 out of 7 endemic species had a greater slope in the NWHI then the MHI. Endemic species tend to be in greater abundance in the NWHI suggesting that this variation in life history is not due to density-dependent processes since this pattern is contrary to expectation.

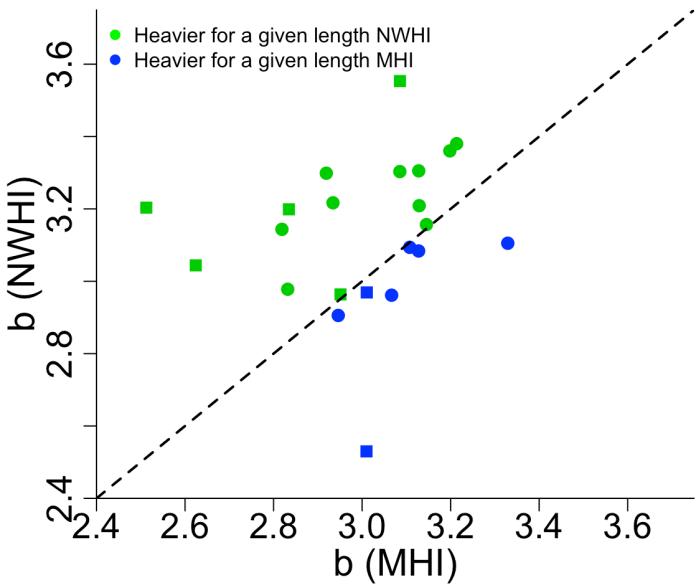



Figure 8. Comparison between slopes for each species in MHI and NWHI. Points above the line represent species with a greater slope in the NWHI (green) and points below the line represent species with a greater slope in MHI (blue). Squares represent endemic species.

Differences in the relationship between weight and length were assessed across time and space for a subset of species with paired comparisons. This is a unique opportunity where a large amount of data on life history attributes of Hawaiian fishes was assembled into a single database allowing for testing hypotheses about changes in condition of Hawaiian reef fishes. Overall the relationship across all species did not change over time, however on average, fishes in the Northwestern Hawaiian Islands (NWHI) were heavier for a given length than in the main Hawaiian Islands (MHI).

Reef fish, Hawai'i Island. Photo: K. Stamoulis

## *Bio-regionalization of Hawaiian fish fauna*

Fish assemblage structure was compared between the NWHI and MHI in ordination space using non-metric multi-dimensional scaling (MDS) analysis coupled with analysis of similarities (ANOSIM) tests (PRIMER v.5, Clarke & Gorley 2001). The data matrix consisted of mean fish biomass or abundance by species at each island in the archipelago. A Bray-Curtis similarity matrix was created from the ln(x+1) transformed mean fish biomass and abundance matrices prior to conducting the MDS.

Fish assemblages were well separated in ordination space based on the nMDS analyses (Figure 9). Analysis by biomass showed greater separation (R = 0.57, $p < 0.01$) then by abundance (R = 0.47, $p < 0.01$). There was high concordance within the MHI by biomass with Ni'ihau and Molokai showing separation from the MHI cluster. Within the NWHI, there was also high concordance with Nihoa, Maro, and Laysan being outliers. Numerical abundance showed less concordance both within and between regions.

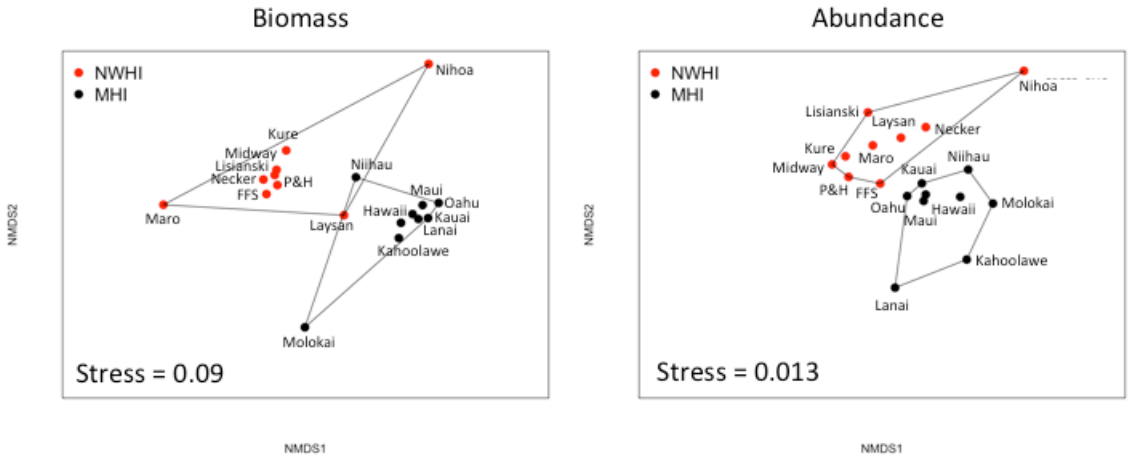



Figure 9. Comparison of fish assemblage structure between the MHI and NWHI. Results of nonmetric multi-dimensional scaling plot of islands by region for (A) biomass ($g/m^2$) and (B) abundance ($\#/m^2$). Minimum convex polygons are drawn around each region for visual purposes. Analysis of similarity (ANOSIM) between MHI and NWHI (A) R=0.57, $p<0.01$, (B) R=0.47, $p<0.01$.

To evaluate the importance of endemic species in the fish assemblage, we created a geographical range index based on information on species' range sizes. We based our geographical range estimates on each species extent of occurrence (EOO), which are drawn from polygons encompassing locations where the species are known to occur based on 169 checklists from around the world. We then calculated the area occupied by each polygon and produced a distribution of these EOOs in 10 quantiles. Distributions in the smallest quantile represent endemic species whose range is limited to the Hawaiian Archipelago.

The distribution of species abundance by range size shows a striking pattern with endemics dominating in the NWHI, particularly around the three most northern islands (Figure 10-11). This distribution flattens out as you move down the chain and is significantly correlated with latitude (Figure 12; $R^2$=0.81, $p$<0.01).

Disproportionate recruitment of endemics at higher-latitude reefs may be related to better growth and survivorship after settlement onto reefs, higher levels of within-reef and regional reseeding at higher latitudes, or other factors (DeMartini and Friedlander 2004).

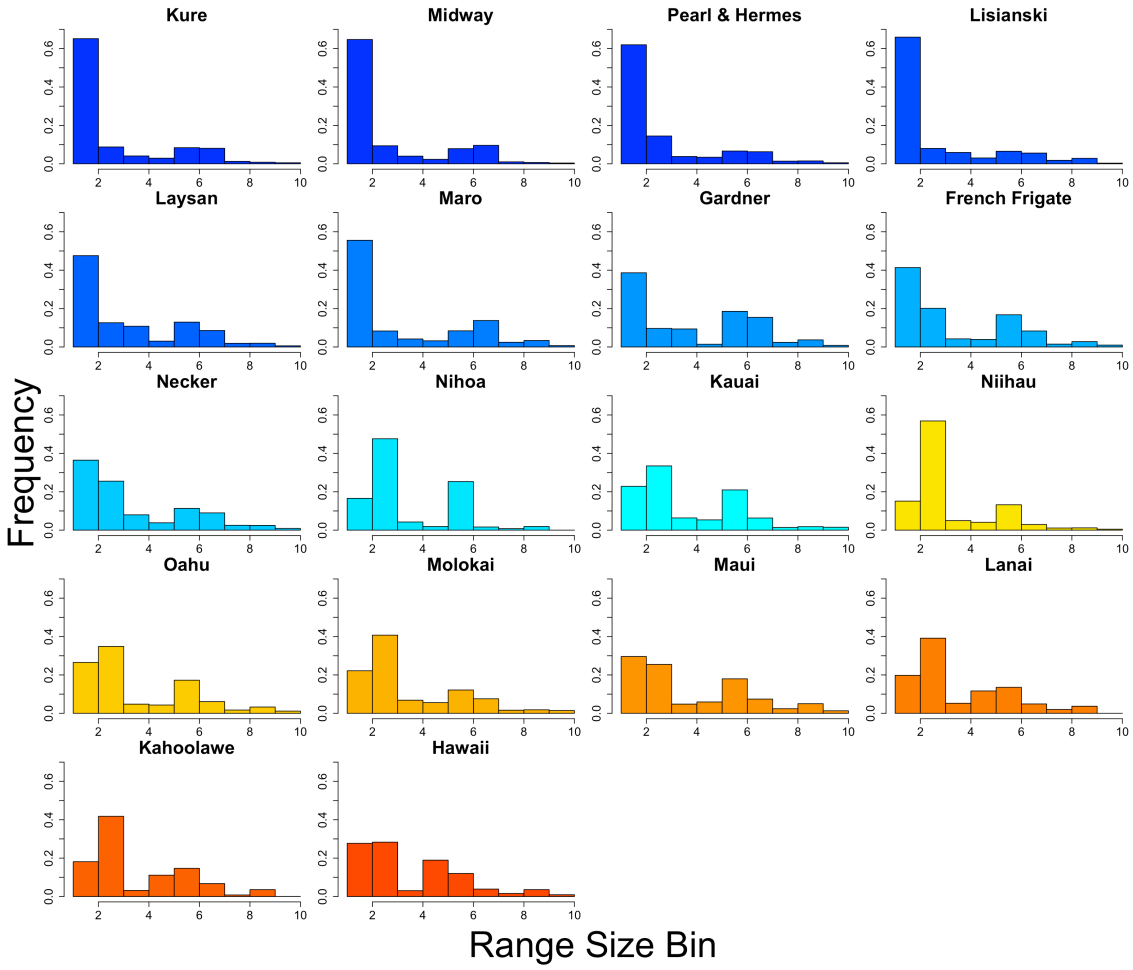



Figure 10. Distribution of numerical abundance of fishes across range sizes throughout the Hawaiian Archipelago. Species range size is binned into 10 even bins ranging from 14.5 x $10^4$ to 24.5 x $10^6$ $km^2$.

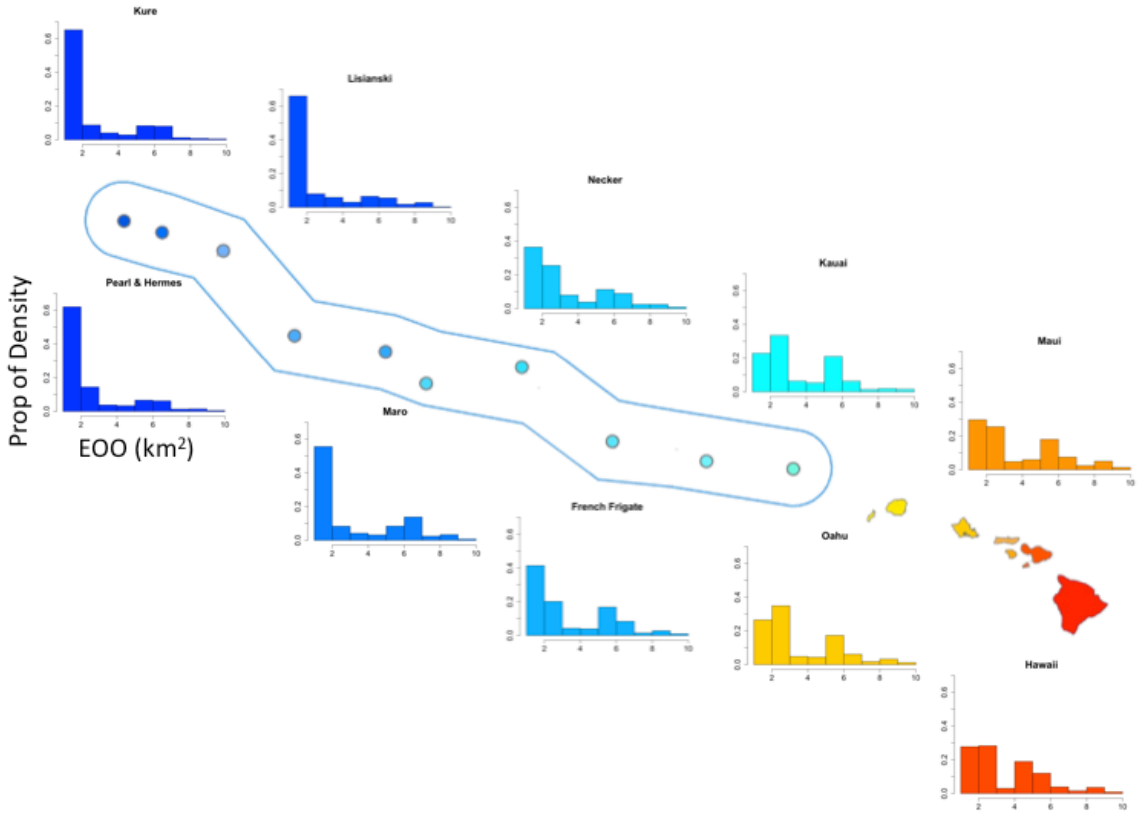



Figure 11. Spatial presentation of the distribution of numerical abundance of fishes across range sizes and the Hawaiian Archipelago.

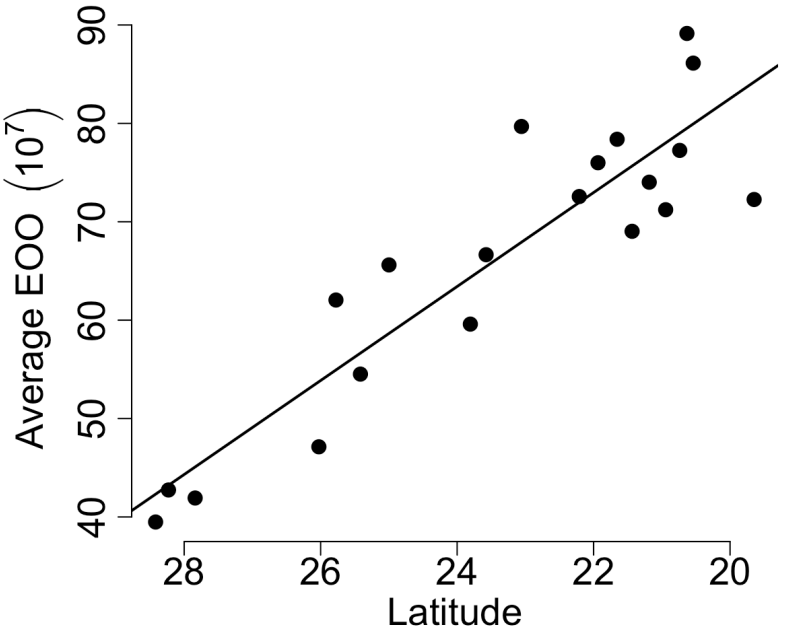



Figure 12. Mean range size of fishes measured as extent of occurrence (EOO) as a function of island latitude ($R^2$=0.81, $p$<0.01).

There is an interesting relationship between endemics and widely ranging Indo-Pacific species (Figure 13). Endemics dominate numerically in the higher latitudes and the switch to dominance by Indo-Pacific species occurs around $25^0$ latitude. This represents an important zoogeographic faunal break in reef fishes within the archipelago.

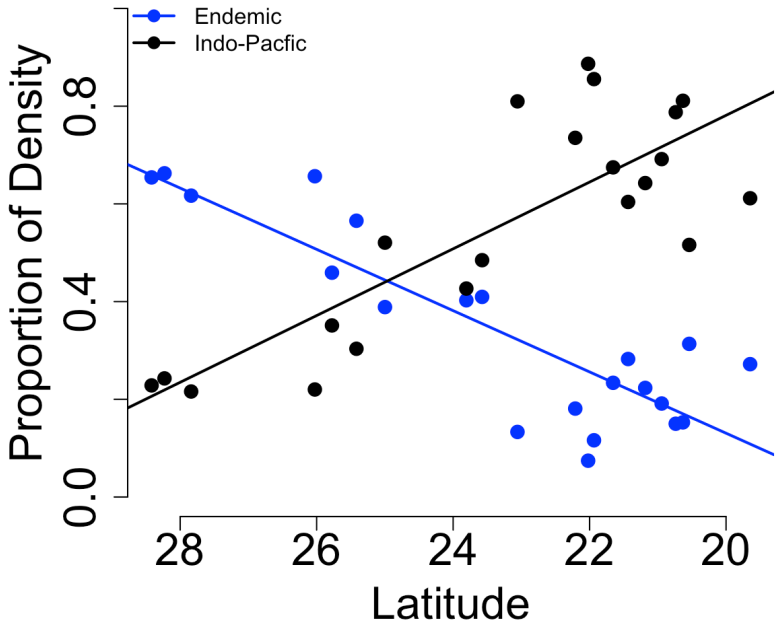



Figure 13. Proportional density of endemics compared to density of fish with Indo-Pacific distributions across latitude.

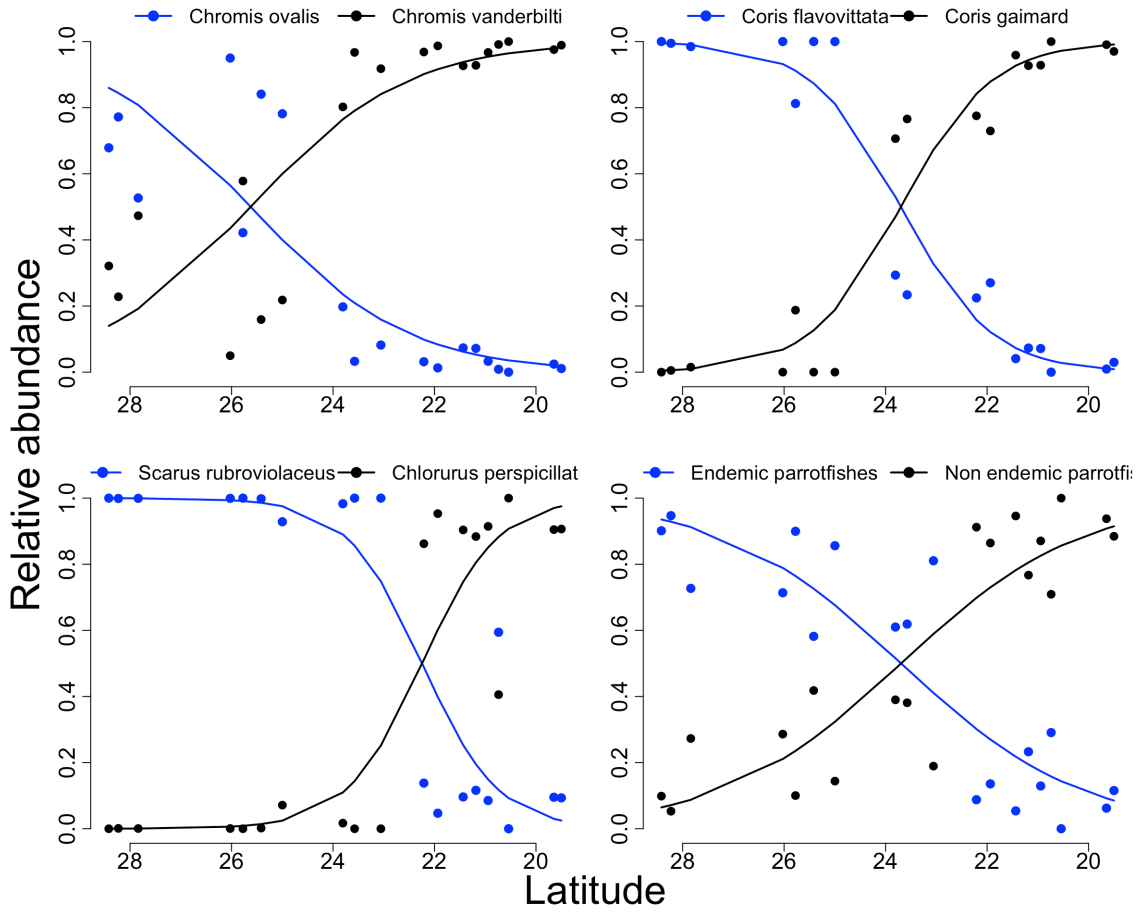



Figure 14. Relative density of endemic species (blue) compared to their wide-ranging relatives (black) across a latitudinal gradient. The Y axis is the relative numerical density for A-C and relative biomass density for D. Lines are fits of a logistic regression for endemic species (blue) and non-endemics (black).

Examination of endemics and their sister species show similar trends and faunal discontinuities (Figure 14). This is true for the genera *Chromis* (a damselfish) and *Coris* (a wrasse); however, parrotfishes show a faunal break further down the chain, with the break occurring between the MHI and NWHI.

Based on the abundance of endemic and non-endemic species, we see several faunal breaks that have important implications for management and our increased understanding of the demography and zoogeography of reef fishes (Figure 15).

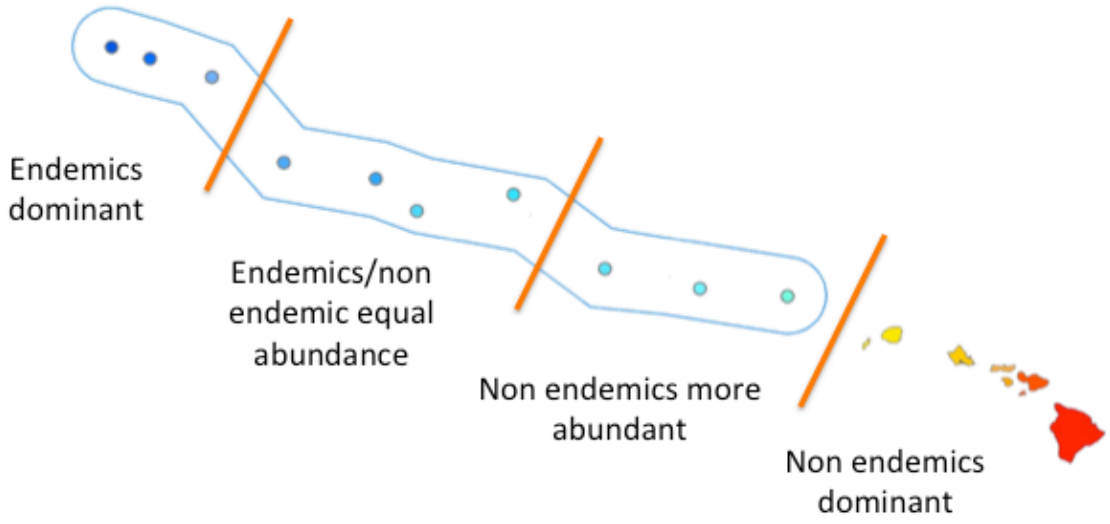



Figure 15. Faunal breaks across the Hawaiian Archipelago based on abundance of endemic and non-endemic fishes.

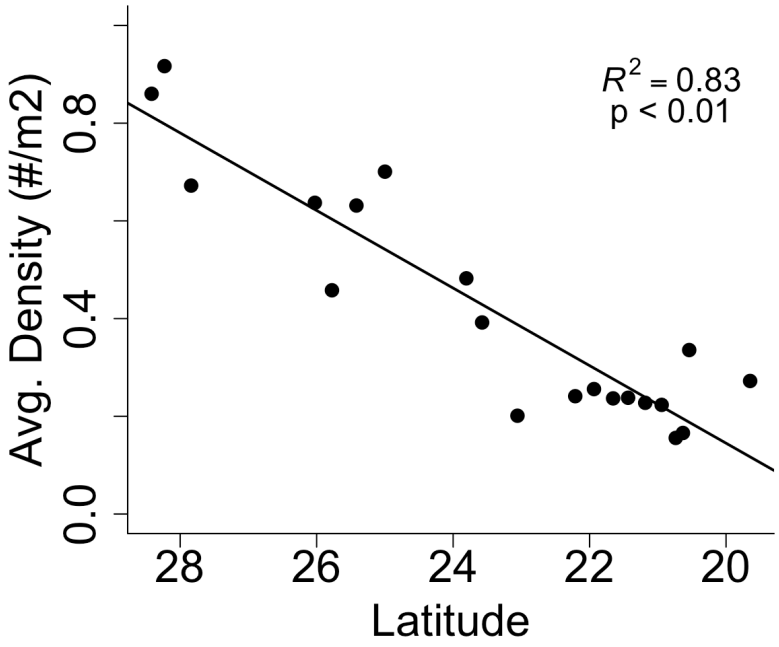



Figure 16. Average density of endemic fish species as a function of latitude ($R^2$=0.83, $p$<0.01)

Endemic species were much more common numerically at the northern end of the chain (Figure 16), accounting for 52-55% of numerical density compared to only 17% on Hawaii Island to the extreme south.

## *Fish assemblage structure across a gradient of human impacts*

Overfishing is thought to be one of the major reasons for coral reef decline around the state and elsewhere. One of the major obstacles to wise management of coral reef fisheries resources is the lack of good information on fish population abundance at spatial scales commensurate with the uses of these resources. Here we describe attributes of fish assemblages across the state and therefore elucidate the spatial patterns of abundance that will help inform proper management and Marine Spatial Planning.

We extend our understanding of the status and structure of fish assemblages across a human impact gradient by comparing metrics based on traditional Hawaiian management boundaries (mokus). This includes comparisons of the relative influences of human population density and physical and anthropogenic factors on distribution, abundance, and size of reef fishes around the state. We also evaluated existing MPAs based on their size and time since establishment.

### *Assessment of stock structure*

Scientific management guidance is lacking for most reef fishes in Hawaii due to the exacting data requirements and many assumptions of conventional stock assessment models. The lack of conventional advice often leads to management paralysis even amidst strong claims about fisheries collapses based on analysis of limited or selective data. We produced unconventional preliminary assessments for 52 species within the main Hawaiian Islands (MHI) by comparing their abundances to the Northwestern Hawaiian Islands (NWHI) Marine National Monument—a large, virtually unfished reference area.

We examined species that were present in the commercial catch database, with an average annual catch of >1000lbs, hereafter referred to as resource species. All but 52 species were removed from full consideration due to a skewed biogeographic distribution—identified using a Spearman rank correlation analysis of biomass densities on latitude throughout the archipelago—inappropriateness of the sampling method (e.g., for schooling coastal pelagic species, extreme habitat specialization or depth range), or inadequate sample sizes (we required observations in at least 20 sites in the NWHI to allow testing for skewed distribution).

Over one-quarter (27%) of the species examined in the main Hawaiian Islands appeared to be depleted below 10% of unfished abundance, while 42% were below 25% of unfished abundance (Figure 17). Large mobile predators were especially affected, but many other resource species appeared to have poor stock condition as well.

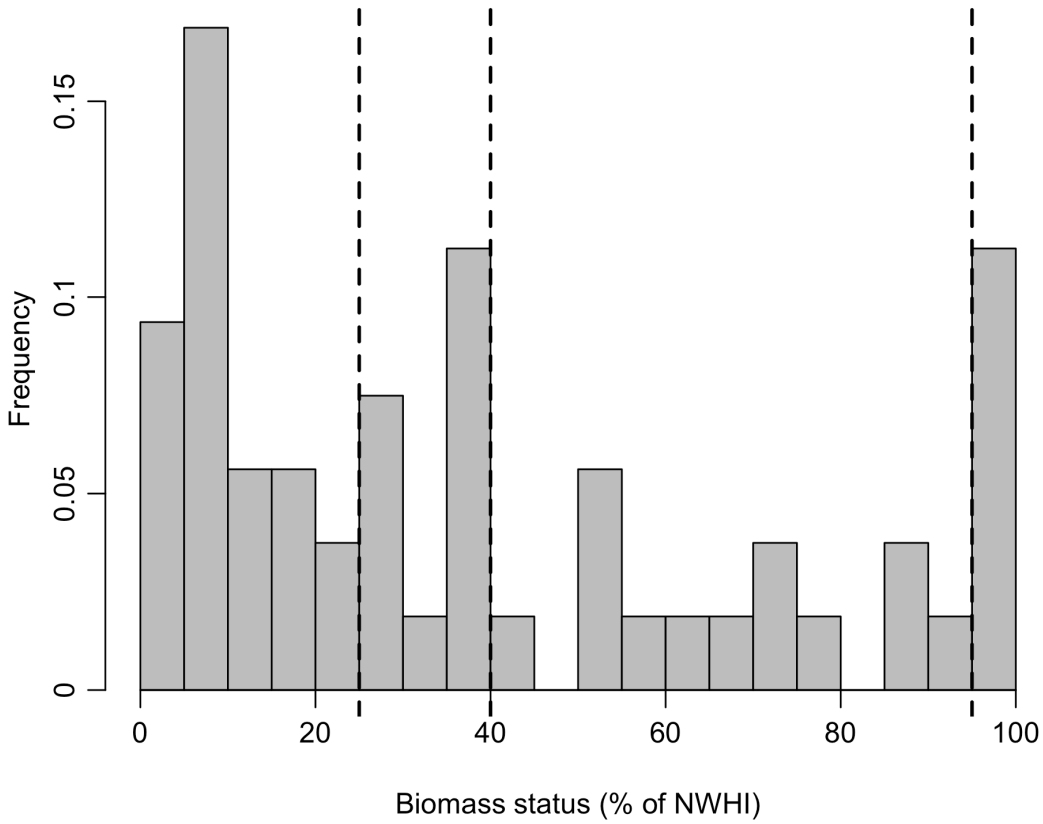



Figure 17. Distribution of stock status estimates for 52 targeted species without a latitudinal bias; biomass status is biomass in the MHI as a percent of the NHWI. Dotted lines represent three status levels, <25% of NWHI are depleted or in critical condition, <40% of NWHI are below desired levels, and >90% of NWHI are hyperabundant.

### *Major drivers of resource fish biomass*

Exploratory analyses of drivers of resource fish biomass were conducted using Boosted Regression Trees (BRT). BRTs are grounded in traditional regression analysis but take advantage of adaptively combining large numbers of regressions in a tree framework that can provide high predictive performance to identify primary variables and their interactions (Elith et al 2008). BRTs were constructed using the routines *gbm* and *gbm.step* in the package *dismo* in the R statistical program version 3.0.0 (R Development Core Team).

A series of habitat and human demographic variables were attributed to individual surveys to input into BRT to evaluate the relative influence of possible drivers of fish assemblage patterns in Hawaii. Multiple habitat metrics were calculated using ArcGIS 10 (ESRI). A 30 m buffer was created for each survey point to quantify habitat metrics. Habitat metrics representing benthic structure were derived from bathymetric surfaces. For the Main Hawaiian Islands, SHOALS LiDAR data (Irish and Lillycrop 1999) was available for the majority of

the survey area and was interpolated at a 5 m resolution. In the Northwestern Hawaiian Islands there was very little LiDAR coverage and multi-beam bathymetry was patchy with sparse coverage in shallow areas. In this case, bathymetry surfaces derived from satellite imagery provided the most complete coverage and were therefore used for calculating habitat metrics. Since this product had a resolution of 4m, it was re-sampled to 5 m to match the MHI data. For each metric, cell values within each site buffer were averaged to create a single measure for each site. Structural metrics included average depth, aspect (slope direction), slope (in degrees), and curvature (slope of slope). These structural metrics have been shown by previous research to influence fish assemblage characteristics in Hawaii and elsewhere (Wedding and Friedlander 2008, Pittman et al. 2011, Stamoulis and Friedlander 2013). Distance to shore (Schmiing et al. 2013) was also calculated for each site.

Benthic cover is another important habitat variable that influences fish assemblages. NOAA's Biogeography Branch has created habitat maps for both the MHI (2007) and NWHI (2003). However, these maps were produced using different methods and have different spatial resolutions. The NWHI maps were produced using an unsupervised (automated) classification method and have a much larger spatial resolution (MMU = 100 $m^2$) compared to the MHI maps (MMU = 1 acre/4047 $m^2$) that were hand digitized using a supervised method. For this reason, the NWHI maps were down-sampled to match the MHI maps, which involved a process of eliminating or aggregating habitat patches smaller than 1 acre. Habitat classes also differed between the maps, so a general classification scheme was developed to make them comparable. Finally, each survey point was attributed with a habitat cover type.

For the purpose of providing relevant spatial comparisons, the traditional Hawaiian district or moku was chosen as a unit of spatial stratification. Mokus roughly correspond to biophysical attributes of island ecosystems such as leeward/windward and wet/dry districts of islands (Malo 1951). At the local (ahupua'a) and district (moku) levels, fishing activities were strictly regulated by a system of rules that were embedded in socio-political structures and religious systems (the kapu system) (Friedlander et al. 2013). While the basic unit of land management was the ahupua'a, the basic unit of marine resource management and harvesting was the moku or district (Davianna McGregor pers. comm.).

While the Hawai'i statewide GIS program (http://planning.hawaii.gov/gis/) provides a GIS shapefile of ahupua'a and moku boundaries, there is no definitive source for this information. The difficulty arises from several factors: 1) Early Hawaiians left no maps, 2) in Hawaiian history, several volcanic eruptions have modified or destroyed ahupua'a and/or moku boundaries, 3) boundaries were well established at the shoreline but more ambiguous upslope and offshore, 4) the conquest and unification of the islands destroyed sovereign boundaries, and 5) current boundaries set by various indigenous and historic authorities are in conflict (Juan Wilson pers. comm.). For these reasons, we found the most

authoritative source for this information to be the Island Breath organization (http://www.islandbreath.org/). In 2010 Island Breath conducted a detailed survey effort using historical documents, early Hawaiian maps, USGS survey maps, individual accounts, and with the support of the Aha Keole Advisory Committee, the Western Pacific Regional Fishery Council (WESPAC), and the Kaua‘i Historic Society. Using these moku maps, each survey location was attributed to the nearest moku land division (Figure 18).

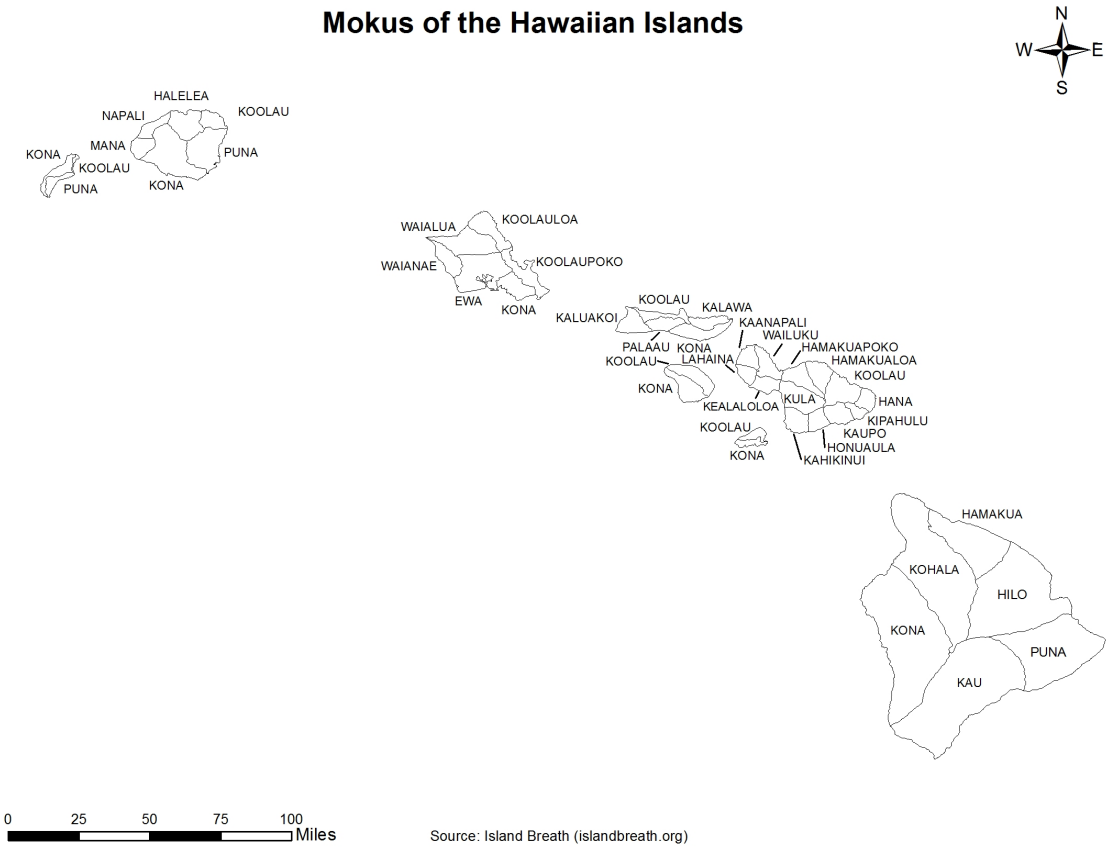



Figure 18. Map of mokus across the main Hawaiian Islands.

Mokus differed widely in terms of attributes such as area, length of shoreline, exposure, human population, and number of boating facilities (Table 3). Not surprisingly, the largest mokus are located on the island of Hawai‘i with Kau and Kona both well over 2,000 square kilometers. The smallest mokus are located on Ni‘ihau and Maui, as well as Kaho‘olawe. With some exceptions the shoreline lengths corresponded with the moku areas. In terms of human population, the O‘ahu mokus had the highest population density by far, with Ewa and Kona encompassing the city of Honolulu and Kapolei/Ewa, respectively. The Kaho‘olawe mokus have no permanent human residents and mokus on Lāna‘i and Ni‘ihau, as well as Kahikinui on Maui had very low human populations. Koolaupoko in southeast O‘ahu had the most boating facilities followed by Kona (O‘ahu), and Puna (Kaua‘i).

Table 3. Attributes of mokus organized by island

| Moku Name | Island | Moku area km$^2$ | Shoreline length km | Exposure | Human population | Boating facilities |
|---|---|---|---|---|---|---|
| KONA HAW | Hawaii | 2,243 | 115 | W | 47,106 | 4 |
| KAU | Hawaii | 2,335 | 103 | S | 8,389 | 2 |
| PUNA HAW | Hawaii | 1,356 | 82 | E | 45,173 | 1 |
| HILO | Hawaii | 1,807 | 66 | E | 51,920 | 4 |
| HAMAKUA | Hawaii | 771 | 50 | N | 9,485 | 0 |
| KOHALA | Hawaii | 1,962 | 72 | W | 20,462 | 3 |
| KONA KAH | Kahoolawe | 53 | 27 | S | 0 | 0 |
| KOOLAU KAH | Kahoolawe | 63 | 26 | N | 0 | 0 |
| MANA | Kauai | 112 | 17 | W | 133 | 0 |
| KONA KAU | Kauai | 524 | 44 | S | 22,392 | 5 |
| PUNA KAU | Kauai | 360 | 37 | E | 32,494 | 6 |
| KOOLAU KAU | Kauai | 109 | 22 | N | 5,985 | 0 |
| HALELEA | Kauai | 232 | 21 | N | 4,152 | 2 |
| NAPALI | Kauai | 101 | 24 | N | 30 | 0 |
| KONA LAN | Lanai | 190 | 40 | W | 2,817 | 2 |
| KOOLAU LAN | Lanai | 176 | 38 | E | 3 | 0 |
| LAHAINA | Maui | 84 | 15 | W | 12,664 | 4 |
| KEALALOLOA | Maui | 111 | 19 | S | 1,234 | 1 |
| KULA | Maui | 282 | 10 | W | 30,344 | 0 |
| HONUAULA | Maui | 149 | 28 | S | 4,214 | 1 |
| KAHIKINUI | Maui | 108 | 13 | S | 10 | 0 |
| KAUPO | Maui | 145 | 15 | S | 108 | 0 |
| KIPAHULU | Maui | 63 | 10 | S | 160 | 0 |
| HANA | Maui | 97 | 21 | E | 1,507 | 1 |
| KOOLAU MAU | Maui | 246 | 21 | N | 450 | 1 |
| HAMAKUALOA | Maui | 164 | 20 | N | 11,434 | 1 |
| HAMAKUAPOKO | Maui | 180 | 13 | N | 19,378 | 0 |
| WAILUKU | Maui | 152 | 27 | E | 52,003 | 1 |
| KAANAPALI | Maui | 111 | 19 | W | 8,805 | 1 |
| KALUAKOI | Molokai | 158 | 39 | S | 695 | 1 |
| PALAAU | Molokai | 118 | 9 | S | 1,209 | 0 |
| KONA MOL | Molokai | 186 | 42 | S | 4,084 | 1 |
| KALAWA | Molokai | 113 | 27 | N | 48 | 0 |
| KOOLAU MOL | Molokai | 104 | 39 | N | 1,099 | 1 |
| KONA NIH | Niihau | 105 | 38 | W | 92 | 0 |
| PUNA NIH | Niihau | 68 | 23 | S | 65 | 0 |
| KOOLAU NIH | Niihau | 12 | 13 | E | 11 | 0 |
| WAIANAE | Oahu | 159 | 29 | W | 47,578 | 2 |
| EWA | Oahu | 461 | 86 | S | 339,568 | 5 |
| KONA OAH | Oahu | 173 | 30 | S | 339,212 | 7 |
| KOOLAUPOKO | Oahu | 207 | 71 | E | 142,866 | 9 |
| KOOLAULOA | Oahu | 211 | 42 | E | 20,829 | 1 |
| WAIALUA | Oahu | 339 | 27 | N | 47,416 | 1 |

Most human related metrics were calculated at the moku scale (Table 3). Average population for each moku was calculated using the 2010 census data. Because census blocks did not correspond with moku boundaries, a 1 ha resolution grid was developed where each cell contained the average population density (pop/ha) for that census block. The cells corresponding to each moku were then sampled and summed to calculate the total population for each moku. Total population of each moku was divided by the shoreline length of that moku to provide an index of fishing pressure (Williams et al. 2008). Thus mokus with large populations and small shorelines were weighted more heavily. The number of boating facilities per moku was also used as an indication of fishing pressure (Williams et al. 2008).

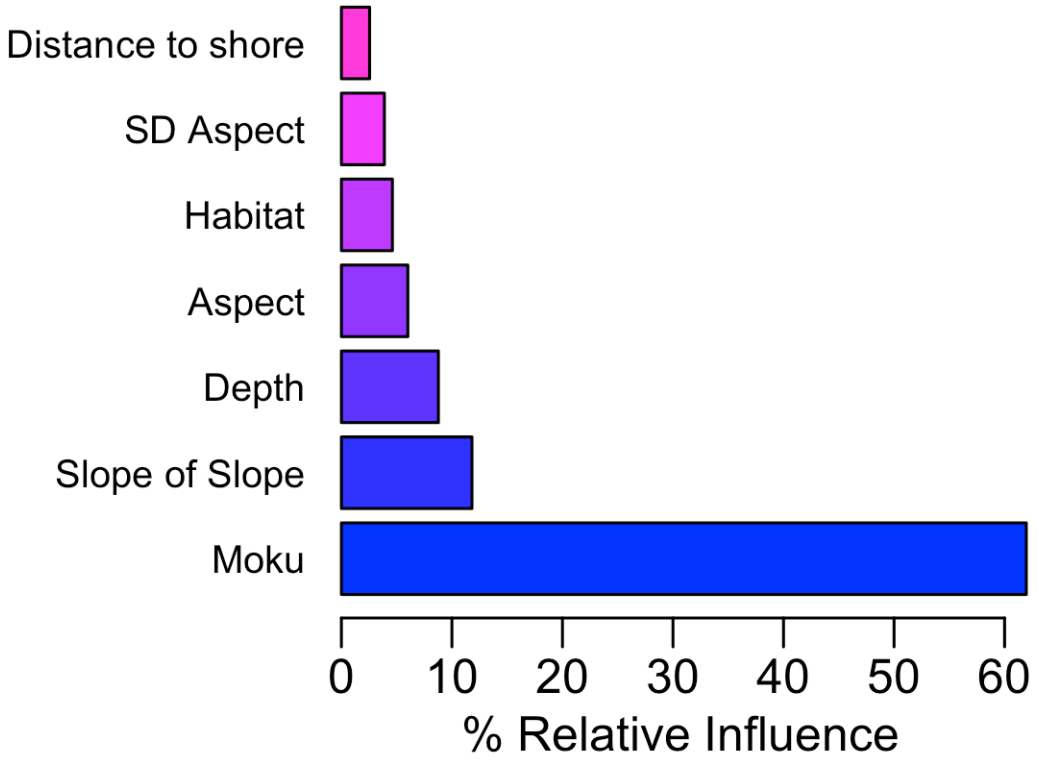



Figure 19. Result of boosted regression tree analysis displaying top 7 variables that explaned the most variance in resource fish biomass in the Main Hawaiian Islands.

A final model from the boosted regression tree analysis resulted in an output of the relative importance or influence of each variable included (Figure 19) with a higher relative influence indicating a stronger effect on resource fish biomass. Overall, the model explained 35% of the total variation in the data with over 60% of the relative variation explained by moku, followed by 12% explained by slope of slope, which has been shown previously to be an important habitat predictor of fish biomass (Wedding and Friedlander 2008, Pittman et al. 2011, Stamoulis and Friedlander 2013).

Total fish biomass was lowest in the mokus around populated areas of Oahu and Maui, with intermediate biomass in more remote locations around the MHI (Figure 20). Obvious differences in apex predator biomass are observed between the MHI and NWHI, with only the most remote locations in the MHI sustaining modest apex predator biomass. Additionally, many of the locations with low overall biomass also had low biomass of herbivores with implications for reef resileince. In fact, many of the locations with low herbivore biomass are also areas where macroalgae is problematic and threatens reef health.

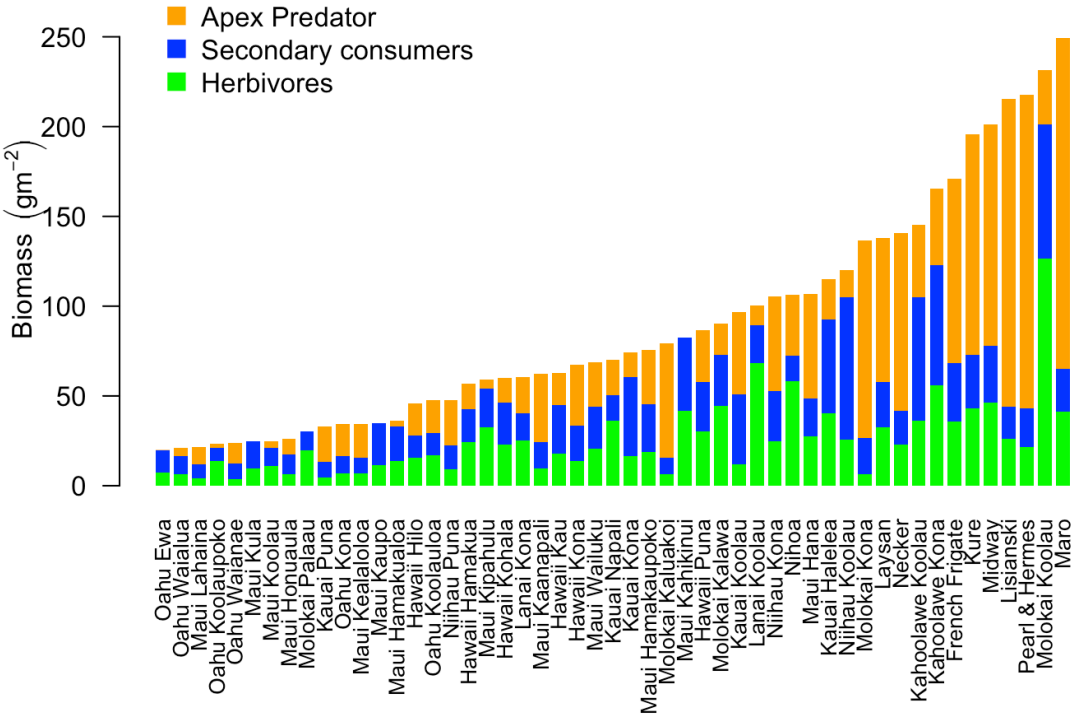



Figure 20. Total fish biomass broken into three trophic categories for each moku in the MHI and island in the NWHI, ordered by total fish biomass.

Biomass of resource species was negatively correlated with human population density among mokus ($r_s$=-0.57, $p$<0.01; Figure 21A-B). We used human population per moku divided by shoreline length for that moku as an index of human population pressure. There was a strong negative binomial relationship between target fish biomass and human population density showing that biomass was quite high in areas with little human population pressure (Figure 21B). Mokus around the populated areas of Oahu and Maui had the lowest biomass of resource fish overall and these locations also had few apex predators. There was a strong negative correlation between target fish biomass and the number of boating facilities per moku ($r_s$=-0.46, $p$<0.01; Figure 21C-D). Target fish biomass was highest in mokus with northern and easterly exposures. Mokus with southern and westerly exposures have less severe sea conditions and these patterns

likely result from greater accessibility and therefore heavier fishing pressure in these locations (Figure 21E-F).

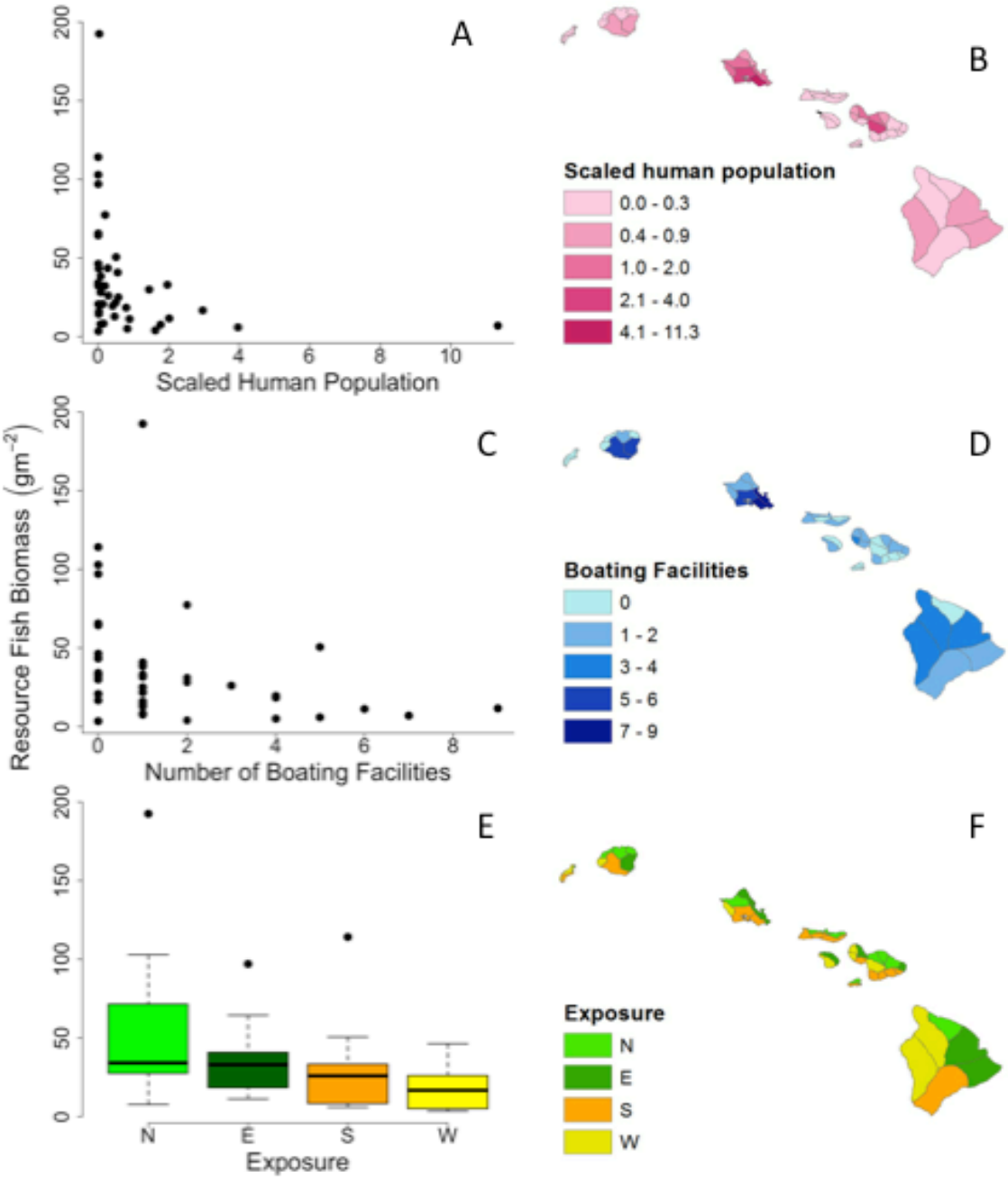



Figure 21. Relationship and spatial representation of resource fish biomass as a function of attirbutes by moku for (A-B) scaled human population (total human population/length of shoreline), (C-D) number of boating facilities, (E-F) exposure to phyiscal conditions (North, East, South, West).

*Comparison of Marine Managed Areas in Main Hawaiian Islands*

Hawaii has a variety of marine managed areas (MMAs) throughout the state that vary greatly in size and shape, and offer various levels of protection from fishing. With the robust dataset compiled here, we evaluated the relative status of MMAs by comparing the level of resource fish biomass among these them.

Marine managed areas in Hawai‘i exhibit a large variety of regulations, mostly related to gear type. For this reason, regulations were standardized to general categories. These included full protection (no fishing or collecting), partial protection (certain gear restricted), restricted access (military areas, Volcano National Park, etc.), and open (no restrictions). Each site was attributed with management “status” according to its location.

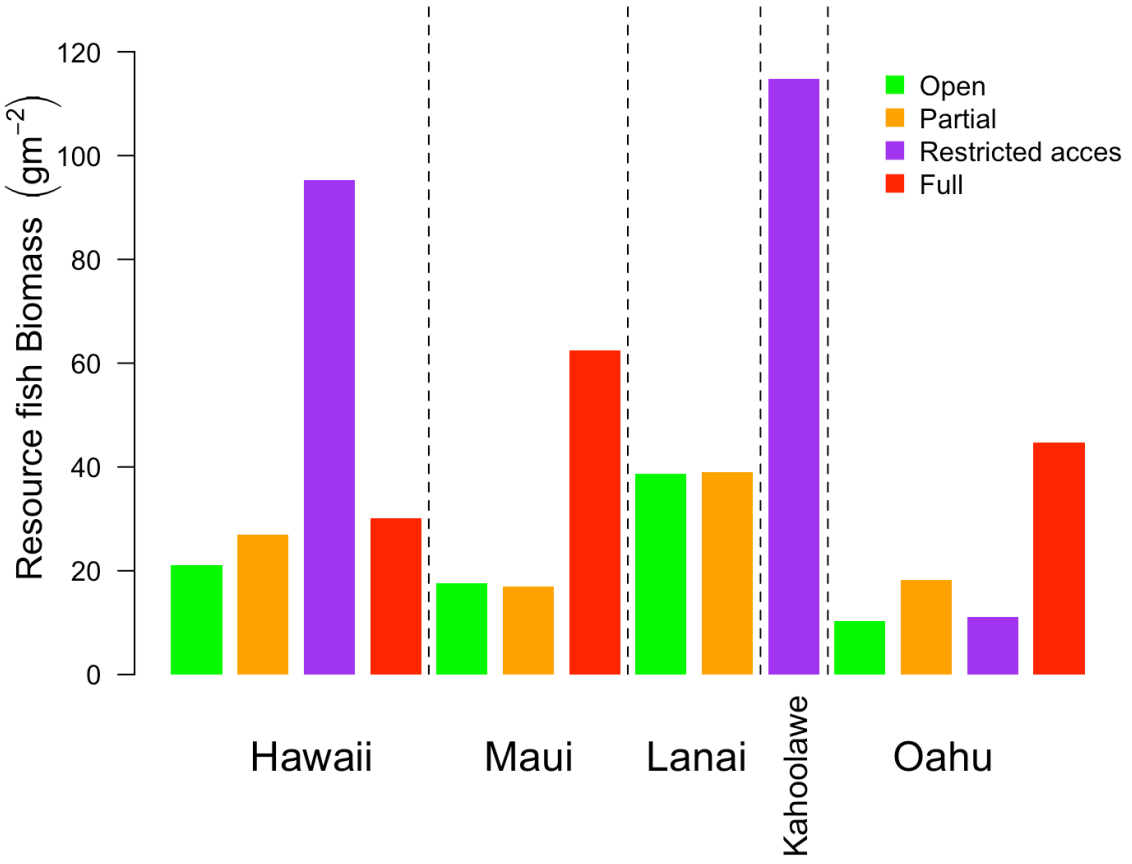



Figure 22. Resource fish biomass by island for 3 levels of spatial protection compared to open areas.

Fully protected MMAs were much more effective than partially protected ones (Figure 22). This was particularly true on Oahu, and to a lesser extent Maui, where fishing pressure is very high outside no-take areas. On Hawaii Island, restricted areas (e.g., Volcano National Park) have biomass equal to or greater

than fully protected areas. However, partially protected areas also afford much lower protection on Hawaii Island.

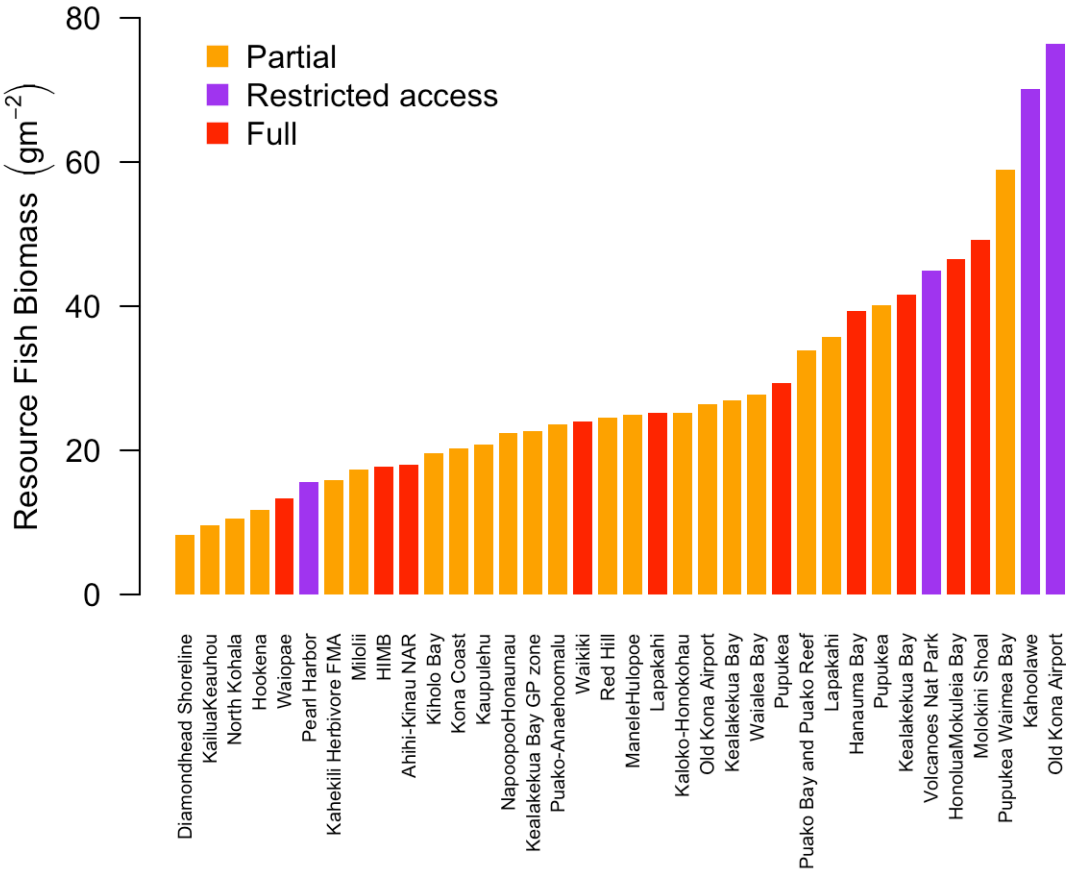



Figure 23. Bar plot of MPAs ordered by resource fish biomass. Colors denote protection level of MPAs

When comparing resource fish biomass by individual managed areas, in some cases restricted access infers the same benefits as full protection (Figure 23). For example, Old Kona airport, on Hawai‘i Island, has the highest average resource fish biomass. This location has dual benefits of protection from both shoreline and boat access. It is also a highly productive area oceanographically, with a steep drop off and strong currents enhancing primary productivity and coral cover. Kaho‘olawe is another example of high biomass and is effectively the state’s largest marine protected area outside the NWHI. Many factors besides level of protection enter into the ability of an MMA to protect and produce high levels of resource fish biomass, including but not limited to MMA total area, area of hard-bottom habitat, age of MMA, and compliance (e.g., amount of poaching).

Another useful way to compare MMA effectiveness is to calculate total standing biomass of resource fishes (Figure 24). This is a function of average biomass and total area of hard-bottom habitat. Thus, MMAs with comparatively low

average biomass may support a large standing stock due to a large area of suitable habitat. This is important because a large standing stock of resource fishes protects genetic and species diversity, and enhances adult and larval spillover in adjacent and "downstream" areas, thereby supporting fisheries (McClanahan and Mangi 2000, Palumbi 2004, Sladek Nowlis and Friedlander 2005). When compared in this way, Ahihi-Kinau Natural Area Reserve in southwest Maui is by far the most effective MMA (Figure 25).

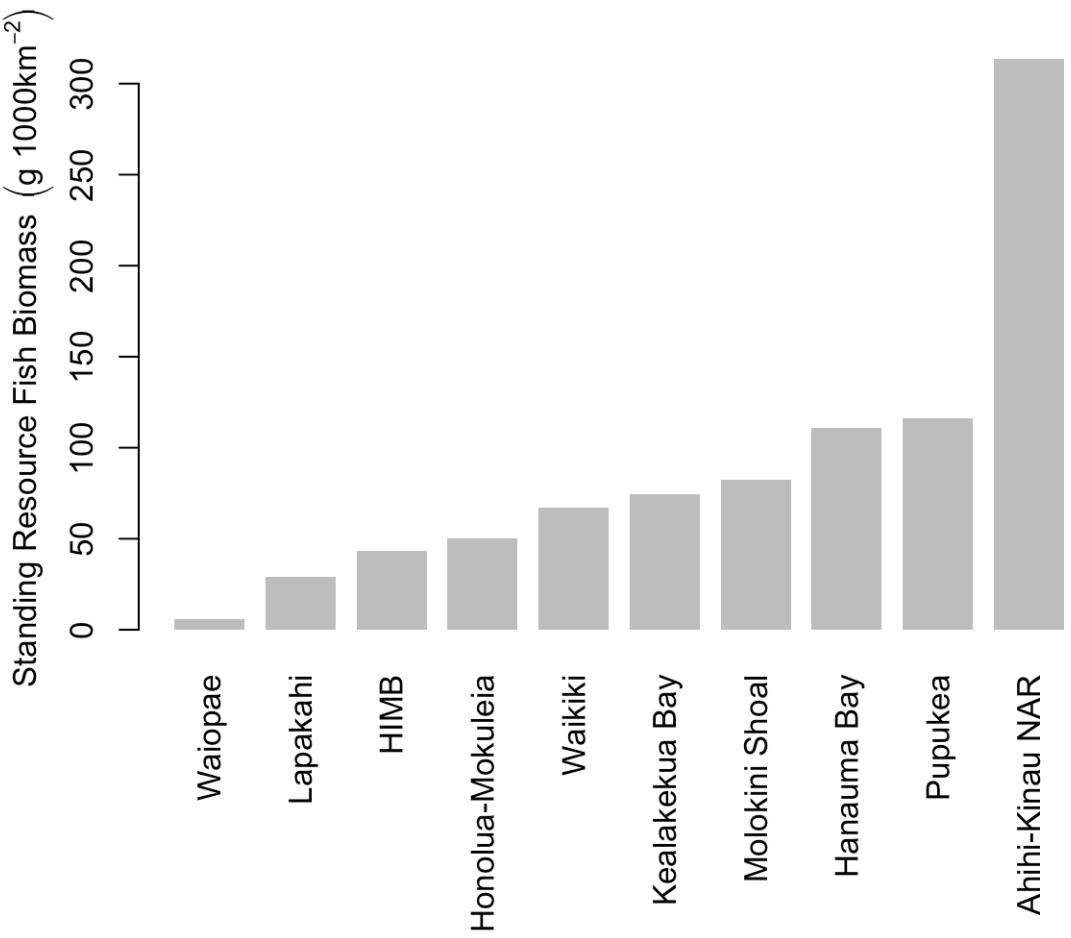



Figure 24. Bar plot of fully protected areas ordered by total resource fish biomass – average transect values multiplied by area of hard-bottom habitat.

MMA age is a primary factor determining effectiveness in producing high biomass of resource fishes. Many reef fish are relatively long-lived so the effects of protection from fishing are delayed but cumulative. This is illustrated by Figure 25, which shows the relationship between MMA age and resource fish biomass. A linear model provided a good fit to this data ($R^2$=0.3, $p$<0.01), though it appears that after about 15 years resource fish biomass begins to increase at a faster rate. This explains why the oldest MPAs in Hawai'i are among the most effective. Hanauma Bay was the first marine protected area in the state, established in 1967. This was followed in short order by Kealakekua Bay (1969) and Ahihi-Kinau NAR (1970).

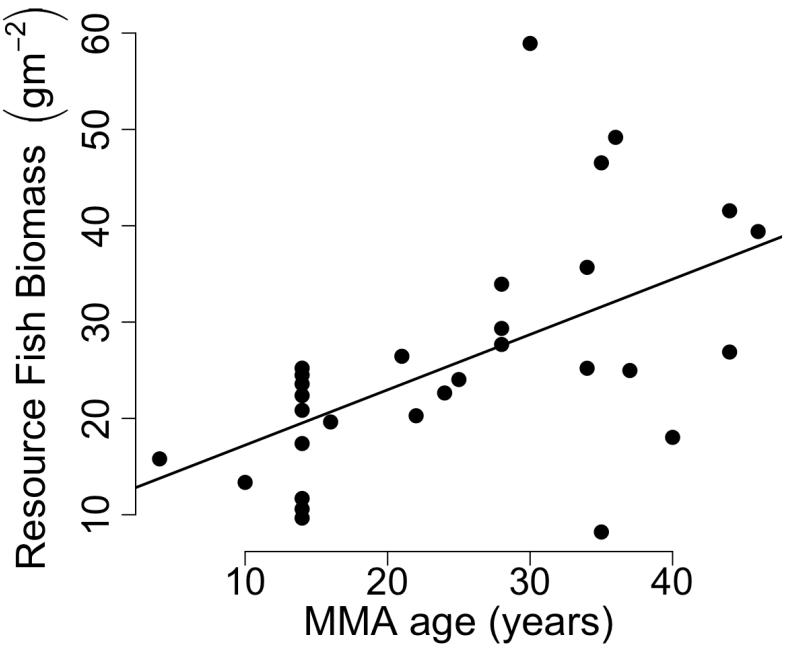



Figure 25. Resource fish biomass vs MMA age in years ($R^2$=0.3, $p$<0.01)

Bigscale Soldierfish -ʻūʻū (Myripristis berndti) Northwestern Hawaiian Islands. Photo: Ryan Okano

## *Discussion*

One of the main requirements of effective management of coral reef fisheries is accurate information on fish populations at spatial scales that correspond to these resource uses. This information is crucial to developing sustainable fisheries management strategies, improving current management approaches such as marine protected areas, informing design of future MMA networks, and aiding in the development of coastal and marine spatial planning (CMSP). There are a number of data sets of visual surveys of reef fishes from around the Hawaiian Islands, representing the work of both government and non-government organizations (eg. NOAA CRED, NOAA Biogeography, DLNR DAR, UH CRAMP, TNC, UH Fisheries Ecology Research Lab). However, no single data set is spatially comprehensive enough to enable a full understanding of the natural and anthropogenic processes that affect the distribution, abundance, and size of reef fish throughout the state. **This research effort has, for the first time, synthesized all of these datasets into a single spatially comprehensive database encompassing the entire Hawaiian archipelago.**

We compiled 25 datasets, representing more than 25,000 individual fish surveys from throughout the island chain since the year 2000. These data were rigorously error checked and integrated into a master database with a standardized structure. A key component of this database is a fish species table containing the most current and up to date information on the life history and ecology (e.g., length-weight parameters, trophic position, movement, and feeding ecology) for each fish species observed on surveys in the Hawaiian Islands. This information is imperative to the accurate assessment, monitoring, and management of coral reef fishes in Hawai‘i and will be made available to the scientific and resource management communities.

With this extensive dataset we developed the first ever bioregionalization of the Hawaiian Archipelago based on the abundance and biomass of reef fishes. Results show clear separation between the Main Hawaiian Islands and the Northwestern Hawaiian Islands, but there are also a number of additional faunal breaks that are driven primarily by the relative abundance of endemic species. Fish species endemic to Hawai‘i (found exclusively in the Hawaiian Archipelago) are much more common at the northern end of the chain and showed a strong and statistically significant correlation with latitude. Higher abundance of endemics at higher-latitude reefs may be related to better growth and survivorship after settlement onto reefs, higher levels of within-reef and regional self-recruitment at higher latitudes, or other factors (DeMartini and Friedlander 2004). These bioregions have important implications for management of reef fisheries at an archipelagic scale, and they further our understanding of the macroecology of reef fishes and their spatial distribution at large spatial scales.

The traditional Hawaiian district or moku was used as a unit of spatial stratification in the Main Hawaiian Islands. Mokus correspond to major

biophysical attributes of island ecosystems and were the basic unit of marine resource management and harvesting in ancient Hawai‘i. We attributed biological, physical, and human demographic information to each moku for analytical purposes and much of the variability in fish assemblage characteristics was explained by moku. We used human population per moku divided by shoreline length as an index of human population pressures. Biomass of fisheries resource species was negatively correlated with human population density among mokus with high biomass occurring in areas with low population pressure. Results highlight that reef fish populations in many areas in Hawaii have been negatively impacted by human population pressure. However, we also found a number of locations in the MHI that have high levels of fish biomass, suggesting that these areas could help replenish more heavily impacted areas if effective management is implemented.

Effectiveness of marine protected areas in Hawai‘i were compared in terms of resource fish biomass. Hawaiian MMAs were categorized into 3 major categories of resource protection: full, partial, open (no protections), and a fourth category was included to represent restricted access areas that function as de-facto MMAs. Results showed that two of these restricted access areas, Old Kona Airport (Hawai‘i Island) and Kaho‘olawe Island, had the highest resource fish biomass per unit area compared with all other MMAs. MMA effectiveness varied due to a number of factors other than level of protection. By comparing total biomass of resource fishes by area of hard-bottom habitat, we found that Ahihi-Kinau Natural Area Reserve in southwestern Maui was by far the most effective MMA. A primary factor determining MMA effectiveness is MMA age or time since establishment. Many reef fishes are long lived so the effects of protection may be delayed as a result. We showed a strong positive relationship between MMA age and resource fish biomass, with older MMAs having higher resource fish biomass. MMAs around the populated areas of O‘ahu and Maui showed higher biomass relative to fished areas. However, overall biomass in these protected areas was lower than MMAs on Hawai‘i Island and Lāna‘i, where overall human pressure is lower.

This report is the first ever synthesis of reef fish data in Hawaii and is an important contribution to our understanding of reef fish ecology and the effects of human impacts on reef fishes in the archipelago. These data are unprecedented in scope and provide the clearest picture of the status of reef fish populations across the entire Hawaiian Archipelago. We definitively show that humans are having a significant negative impact on reef fish populations in Hawaii and urgent management is necessary. MPAs have been shown to be effective, particularly in more populated areas. Community managed areas have also been shown to be effective in less populated areas where strong community values still exist. Owing to the failures of conventional marine management in the Hawaiian Islands, there is a growing interest in exploring new approaches to conserve marine ecosystems and coastal resources for future generations (Friedlander et al. 2013). Such approaches include shifts towards ecosystem-based

management, increasing local understanding of marine resources, and integrating traditional ecological knowledge and customary management practices into contemporary marine management. Collectively these measures can lead to sustainable resource use for generations into the future.

Spectacled Parrotfish – uhu uliuli (*Chlorurus perspicillatus*) Northwestern Hawaiian Islands. Photo: K. Stamoulis

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Appendix I. List of fish species encountered on underwater visual surveys and attributes used in this study including: ***Zoogeographical category*** describing the species distribution following Randall's definitions where 1- circumglobal, 2- wide-ranging Indo-Pacific, 3- Eastern tropical Pacific, 4- Japan to Hawaii, 5- antitropical, 6- Central Pacific, 7- waif, and 8- endemic; ***Trophic 9*** with trophic levels broken into 9 categories where Z- zooplanktivore, Hgd- herbivore grazer/detritivore, Hscex- herbivore scraper/excavator, Hbrow- herbivore browser, Hother- other herbivores, C- corallivore, D- detritivore, MI- mobile invertivore, SI- sessile invertivore, and P- piscivore; ***Trophic 5*** with trophic levels broken into 5 levels where APEX- apex predator, P- piscivore, S- secondary consumer, H- herbivore, Z- zooplanktivore; ***Endemic*** breaks species into 3 groups where E- endemic, I- not endemic, and X- invasive; ***Mobility*** are categorized following Friedlander (1998); ***Resource species*** include those targeted in commercial and recreational catches not including aquarium targets; ***Harvested species*** are resource species plus aquarium targets.

| Family | Species | Zoogeog | Trophic 9 | Trophic 5 | Endemic | Mobility | Resource Species | HarvestedSpecies |
|---|---|---|---|---|---|---|---|---|
| Pomacentridae | *Abudefduf abdominalis* | 8 | Z | Z | E | S1 | TRUE | TRUE |
| Pomacentridae | *Abudefduf sordidus* | 2 | Hother | H | I | S1 | FALSE | FALSE |
| Pomacentridae | *Abudefduf vaigiensis* | 2 | Z | Z | I | S1 | FALSE | FALSE |
| Acanthuridae | *Acanthurus achilles* | 2 | Hgd | H | I | S1 | TRUE | TRUE |
| Acanthuridae | *Acanthurus blochii* | 2 | Hgd | H | I | S2 | TRUE | TRUE |
| Acanthuridae | *Acanthurus dussumieri* | 2 | Hgd | H | I | S2 | TRUE | TRUE |
| Acanthuridae | *Acanthurus guttatus* | 2 | Hgd | H | I | S2 | TRUE | TRUE |
| Acanthuridae | *Acanthurus leucopareius* | 5 | Hgd | H | I | S2 | TRUE | TRUE |
| Acanthuridae | *Acanthurus lineatus* | 2 | Hother | H | I | S1 | FALSE | FALSE |
| Acanthuridae | *Acanthurus maculiceps* | 2 | Hother | H | I | S1 | FALSE | FALSE |
| Acanthuridae | *Acanthurus nigricans* | 2 | Hgd | H | I | S1 | FALSE | FALSE |
| Acanthuridae | *Acanthurus nigrofuscus* | 2 | Hgd | H | I | S1 | FALSE | FALSE |
| Acanthuridae | *Acanthurus nigroris* | 2 | Hgd | H | I | S2 | TRUE | TRUE |
| Acanthuridae | *Acanthurus olivaceus* | 2 | Hgd | H | I | S2 | TRUE | TRUE |
| Acanthuridae | *Acanthurus species* | 2 | Hother | H | I | S1 | FALSE | FALSE |
| Acanthuridae | *Acanthurus thompsoni* | 2 | Z | Z | I | S1 | FALSE | FALSE |
| Acanthuridae | *Acanthurus triostegus* | 2 | Hgd | H | I | S2 | TRUE | TRUE |
| Acanthuridae | *Acanthurus xanthopterus* | 2 | Hgd | H | I | S2 | TRUE | TRUE |
| Mobulidae | *Aetobatus narinari* | 1 | MI | S | I | T | FALSE | FALSE |
| Albulidae | *Albula glossodonta* | 2 | MI | S | I | T | TRUE | TRUE |
| Carangidae | *Alectis ciliaris* | 1 | P | APEX | I | T | TRUE | TRUE |
| Monacanthidae | *Aluterus scriptus* | 1 | Hother | H | I | S2 | TRUE | TRUE |
| Cirrhitidae | *Amblycirrhitus bimacula* | 2 | MI | S | I | R | FALSE | FALSE |
| Ammodytidae | *Ammodytoides pylei* | 8 | SI | S | E | S2 | FALSE | FALSE |

| Family | Species | Zoogeog | Trophic 9 | Trophic 5 | Endemic | Mobility | Resource Species | HarvestedSpecies |
|---|---|---|---|---|---|---|---|---|
| Labridae | *Anampses chrysocephalus* | 8 | MI | S | E | S1 | FALSE | FALSE |
| Labridae | *Anampses cuvier* | 8 | MI | S | E | S1 | TRUE | TRUE |
| Labridae | *Anampses species* | 8 | MI | S | E | S1 | FALSE | FALSE |
| Antennariidae | *Antennarius commersoni* | 2 | P | P | I | R | FALSE | FALSE |
| Antennariidae | *Antennarius drombus* | 8 | P | P | E | R | FALSE | FALSE |
| Anthias (Serranid) | *Anthias species* | 8 | Z | Z | E | S1 | FALSE | FALSE |
| Lutjanidae | *Aphareus furca* | 2 | P | P | I | T | TRUE | TRUE |
| Apogonidae | *Apogon erythrinus* | 8 | MI | S | E | R | FALSE | FALSE |
| Apogonidae | *Apogon kallopterus* | 2 | MI | S | I | R | FALSE | FALSE |
| Apogonidae | *Apogon maculiferus* | 8 | MI | S | E | R | FALSE | FALSE |
| Apogonidae | *Apogon species* | 2 | MI | S | I | R | FALSE | FALSE |
| Apogonidae | *Apogonichthys perdix* | 2 | MI | S | I | R | FALSE | FALSE |
| Pomacanthidae | *Apolemichthys arcuatus* | 8 | SI | S | E | S1 | FALSE | FALSE |
| Lutjanidae | *Aprion virescens* | 2 | P | APEX | I | T | TRUE | TRUE |
| Congridae | *Ariosoma fasciatum* | 2 | P | S | I | R | FALSE | FALSE |
| Tetraodontidae | *Arothron hispidus* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Tetraodontidae | *Arothron meleagris* | 2 | C | S | I | S1 | FALSE | FALSE |
| Gobiidae | *Asterropteryx semipunctatus* | 2 | SI | S | I | S1 | FALSE | FALSE |
| Atherinidae | *Atherinomorus insularum* | 8 | Z | Z | E | T | FALSE | FALSE |
| Aulostomidae | *Aulostomus chinensis* | 2 | P | P | I | S2 | FALSE | FALSE |
| Balistidae | *Balistes polylepis* | 7 | MI | S | I | T | FALSE | FALSE |
| Balistidae | *Balistes species* | 2 | MI | S | I | S2 | FALSE | FALSE |
| Gobiidae | *Bathygobius cocosensis* | 2 | SI | S | I | R | FALSE | FALSE |
| Belonidae | *Belonidae species* | 2 | P | P | I | T | FALSE | FALSE |
| Blenniidae | *Blenniella gibbifrons* | 2 | Hother | H | I | R | FALSE | FALSE |
| Blenniidae | *Blenniidae species* | 2 | Hother | H | I | R | FALSE | FALSE |
| Labridae | *Bodianus albotaeniatus* | 8 | MI | S | E | S2 | TRUE | TRUE |
| Bothidae | *Bothus mancus* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Bothidae | *Bothus pantherinus* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Bothidae | *Bothus species* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Ophidiidae | *Brotula multibarbata* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Callionymidae | *Callionymus comptus* | 8 | MI | S | E | S1 | FALSE | FALSE |

| Family | Species | Zoogeog | Trophic 9 | Trophic 5 | Endemic | Mobility | Resource Species | HarvestedSpecies |
|---|---|---|---|---|---|---|---|---|
| Callionymidae | *Callionymus decoratus* | 8 | MI | S | E | S1 | FALSE | FALSE |
| Scaridae | *Calotomus species* | 2 | Hother | H | I | S2 | TRUE | TRUE |
| Scaridae | *Calotomus carolinus* | 2 | Hbrow | H | I | S2 | TRUE | TRUE |
| Scaridae | *Calotomus zonarchus* | 8 | Hbrow | H | E | S2 | TRUE | TRUE |
| Monacanthidae | *Cantherhines dumerilii* | 2 | C | S | I | S1 | FALSE | FALSE |
| Monacanthidae | *Cantherhines sandwichiensis* | 8 | Hother | H | E | S1 | FALSE | FALSE |
| Monacanthidae | *Cantherhines verecundus* | 8 | Hother | H | E | S1 | FALSE | FALSE |
| Balistidae | *Canthidermis maculatus* | 1 | Z | Z | I | H | FALSE | FALSE |
| Tetraodontidae | *Canthigaster amboinensis* | 2 | Hother | H | I | S1 | FALSE | FALSE |
| Tetraodontidae | *Canthigaster coronata* | 2 | SI | S | I | S1 | FALSE | FALSE |
| Tetraodontidae | *Canthigaster epilampra* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Tetraodontidae | *Canthigaster jactator* | 8 | Hother | H | E | S1 | FALSE | TRUE |
| Tetraodontidae | *Canthigaster rivulata* | 2 | Hother | H | I | S1 | FALSE | FALSE |
| Tetraodontidae | *Canthigaster solandri* | 2 | Hother | H | I | S1 | FALSE | FALSE |
| Tetradontidae | *Canthigaster species* | 2 | Hother | H | I | S1 | FALSE | FALSE |
| Caracanthidae | *Caracanthus typicus* | 8 | MI | S | E | R | FALSE | FALSE |
| Carangidae | *Carangoides ferdau* | 2 | MI | APEX | I | T | TRUE | TRUE |
| Carangidae | *Carangoides orthogrammus* | 2 | P | APEX | I | T | TRUE | TRUE |
| Carangidae | *Caranx ignobilis* | 2 | P | APEX | I | T | TRUE | TRUE |
| Carangidae | *Caranx lugubris* | 1 | P | APEX | I | T | TRUE | TRUE |
| Carangidae | *Caranx melampygus* | 2 | P | APEX | I | T | TRUE | TRUE |
| Carangidae | *Caranx sexfasciatus* | 2 | P | APEX | I | T | TRUE | TRUE |
| Carangidae | *Caranx species* | 2 | P | APEX | I | T | TRUE | TRUE |
| Carcharhinidae | *Carcharhinus amblyrhynchos* | 2 | P | APEX | I | T | FALSE | FALSE |
| Carcharhinidae | *Carcharhinus galapagensis* | 1 | P | APEX | I | T | FALSE | FALSE |
| Carcharhinidae | *Carcharhinus melanopterus* | 2 | P | APEX | I | T | FALSE | FALSE |
| Pomacanthidae | *Centropyge fisheri* | 2 | Hother | H | I | S1 | FALSE | TRUE |
| Pomacanthidae | *Centropyge flavissima* | 7 | Hother | H | X | R | FALSE | FALSE |
| Pomacanthidae | *Centropyge interrupta* | 4 | Hother | H | I | R | FALSE | FALSE |
| Pomacanthidae | *Centropyge loriculus* | 2 | Hother | H | I | R | FALSE | FALSE |
| Pomacanthidae | *Centropyge potteri* | 8 | Hother | H | E | R | FALSE | TRUE |
| Serranidae | *Cephalopholis argus* | 2 | P | P | X | S1 | TRUE | TRUE |

| Family | Species | Zoogeog | Trophic 9 | Trophic 5 | Endemic | Mobility | Resource Species | HarvestedSpecies |
|---|---|---|---|---|---|---|---|---|
| Chaetodontidae | *Chaetodon auriga* | 2 | SI | S | I | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon citrinellus* | 2 | C | S | I | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon ephippium* | 2 | MI | S | I | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon fremblii* | 8 | SI | S | E | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon kleinii* | 2 | Z | Z | I | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon lineolatus* | 2 | SI | S | I | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon lunula* | 2 | SI | S | I | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon lunulatus* | 2 | C | S | I | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon miliaris* | 8 | Z | Z | E | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon multicinctus* | 8 | C | S | E | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon ornatissimus* | 2 | C | S | I | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon quadrimaculatus* | 5 | C | S | I | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon reticulatus* | 2 | C | S | I | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon tinkeri* | 6 | SI | S | I | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon trifascialis* | 2 | C | S | I | S1 | FALSE | TRUE |
| Chaetodontidae | *Chaetodon unimaculatus* | 2 | C | S | I | S1 | FALSE | TRUE |
| Chanidae | *Chanos chanos* | 2 | Hother | H | I | T | TRUE | TRUE |
| Labridae | *Cheilio inermis* | 2 | MI | S | I | S2 | FALSE | FALSE |
| Cheilodactylidae | *Goniistius vittatus* | 8 | SI | S | E | S2 | FALSE | FALSE |
| Scaridae | *Chlorurus perspicillatus* | 8 | Hscex | H | E | S2 | TRUE | TRUE |
| Scaridae | *Chlorurus species* | 2 | Hother | H | I | S2 | TRUE | TRUE |
| Scaridae | *Chlorurus spilurus* | 2 | Hscex | H | I | S2 | TRUE | TRUE |
| Pomacentridae | *Chromis acares* | 2 | Z | Z | I | R | FALSE | FALSE |
| Pomacentridae | *Chromis agilis* | 2 | Z | Z | I | R | FALSE | FALSE |
| Pomacentridae | *Chromis hanui* | 8 | Z | Z | E | R | FALSE | FALSE |
| Pomacentridae | *Chromis leucura* | 2 | Z | Z | I | R | FALSE | FALSE |
| Pomacentridae | *Chromis ovalis* | 8 | Z | Z | E | R | FALSE | FALSE |
| Pomacentridae | *Chromis vanderbilti* | 2 | Z | Z | I | R | FALSE | FALSE |
| Pomacentridae | *Chromis verater* | 8 | Z | Z | E | R | FALSE | FALSE |
| Labridae | *Cirrhilabrus jordani* | 8 | Z | Z | E | S1 | FALSE | FALSE |
| Cirrhitidae | *Cirrhitops fasciatus* | 5 | MI | S | I | R | FALSE | FALSE |
| Cirrhitidae | *Cirrhitus pinnulatus* | 2 | MI | S | I | S1 | FALSE | FALSE |

| Family | Species | Zoogeog | Trophic 9 | Trophic 5 | Endemic | Mobility | Resource Species | HarvestedSpecies |
|---|---|---|---|---|---|---|---|---|
| Blenniidae | *Cirripectes obscurus* | 8 | Hother | H | E | R | FALSE | FALSE |
| Blenniidae | *Cirripectes species* | 8 | Hother | H | I | R | FALSE | FALSE |
| Blenniidae | *Cirripectes vanderbilti* | 8 | Hother | H | E | R | FALSE | FALSE |
| Congridae | *Conger cinereus marginatus* | 8 | P | P | I | R | FALSE | FALSE |
| Congridae | *Conger species* | 8 | P | S | I | R | FALSE | FALSE |
| Labridae | *Coris ballieui* | 8 | MI | S | E | S1 | FALSE | FALSE |
| Labridae | *Coris flavovittata* | 8 | MI | S | E | S2 | TRUE | TRUE |
| Labridae | *Coris gaimard* | 2 | MI | S | I | S1 | FALSE | TRUE |
| Labridae | *Coris venusta* | 8 | MI | S | E | S1 | FALSE | FALSE |
| Gobiidae | *Coryphopterus duospilus* | 2 | Hother | H | I | S1 | FALSE | FALSE |
| Gobiidae | *Coryphopterus species* | 2 | Hother | H | I | S1 | FALSE | FALSE |
| Acanthuridae | *Ctenochaetus hawaiiensis* | 2 | D | S | I | S1 | TRUE | TRUE |
| Acanthuridae | *Ctenochaetus strigosus* | 8 | D | S | I | S1 | TRUE | TRUE |
| Labridae | *Cymolutes lecluse* | 8 | MI | S | E | S1 | FALSE | FALSE |
| Labridae | *Cymolutes praetextatus* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Dactylopteridae | *Dactyloptena orientalis* | 2 | MI | S | I | T | FALSE | FALSE |
| Pomacentridae | *Dascyllus albisella* | 8 | Z | Z | E | S1 | FALSE | TRUE |
| Dasyatidae | *Dasyatis lata* | 8 | MI | S | E | T | FALSE | FALSE |
| Carangidae | *Decapterus macarellus* | 1 | Z | Z | I | T | TRUE | TRUE |
| Carangidae | *Decapterus species* | 1 | Z | Z | I | T | TRUE | FALSE |
| Scorpaenidae | *Dendrochirus barberi* | 8 | MI | S | E | R | FALSE | FALSE |
| Diodontidae | *Diodon holocanthus* | 1 | MI | S | I | S1 | FALSE | FALSE |
| Diodontidae | *Diodon hystrix* | 1 | MI | S | I | S1 | FALSE | FALSE |
| Syngnathidae | *Doryrhamphus excisus* | 2 | Z | Z | I | S1 | FALSE | FALSE |
| Echeneidae | *Echeneis naucrates* | 1 | Z | S | I | T | FALSE | FALSE |
| Muraenidae | *Echidna nebulosa* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Carangidae | *Elagatis bipinnulata* | 1 | P | APEX | I | T | TRUE | TRUE |
| Elopidae | *Elops hawaiensis* | 1 | MI | S | I | T | TRUE | FALSE |
| Muraenidae | *Enchelycore pardalis* | 2 | P | S | I | R | FALSE | FALSE |
| Muraenidae | *Enchelynassa canina* | 2 | P | P | I | R | FALSE | FALSE |
| Engraulidae | *Encrasicholina purpurea* | 8 | Z | Z | E | T | FALSE | FALSE |
| Tripterygiidae | *Enneapterygius atriceps* | 8 | Hother | H | E | S1 | FALSE | FALSE |

| Family | Species | Zoogeog | Trophic 9 | Trophic 5 | Endemic | Mobility | Resource Species | HarvestedSpecies |
|---|---|---|---|---|---|---|---|---|
| Blenniidae | *Entomacrodus marmoratus* | 8 | Hother | H | E | R | FALSE | FALSE |
| Labridae | *Epibulus insidiator* | 2 | MI | S | I | S2 | FALSE | FALSE |
| Serranidae | *Epinephelus quernus* | 8 | P | APEX | E | S1 | TRUE | TRUE |
| Scombridae | *Euthynnus affinis* | 2 | P | APEX | I | T | TRUE | TRUE |
| Gobiidae | *Eviota epiphanes* | 2 | Hother | H | I | S1 | FALSE | FALSE |
| Pentacerotidae | *Evistias acutirostris* | 5 | MI | S | I | T | FALSE | FALSE |
| Blenniidae | *Exallias brevis* | 2 | C | S | I | R | FALSE | FALSE |
| Fistulariidae | *Fistularia commersonii* | 2 | P | P | I | S2 | TRUE | TRUE |
| Apogonidae | *Foa brachygramma* | 8 | MI | S | I | R | FALSE | FALSE |
| Chaetodontidae | *Forcipiger flavissimus* | 2 | SI | S | I | S1 | FALSE | TRUE |
| Chaetodontidae | *Forcipiger longirostris* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Pomacanthidae | *Genicanthus personatus* | 8 | Z | Z | E | S1 | FALSE | FALSE |
| Carangidae | *Gnathanodon speciosus* | 2 | MI | S | I | T | TRUE | TRUE |
| Gobiidae | *Gnatholepis anjerensis* | 2 | Hother | H | I | S1 | FALSE | FALSE |
| Gobiidae | *Gnatholepis caurensis hawaiiensis* | 8 | Hother | H | E | S1 | FALSE | FALSE |
| Gobiidae | *Gobiidae species* | 2 | SI | S | I | S1 | FALSE | FALSE |
| Labridae | *Gomphosus varius* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Microdesmidae | *Gunnellichthys curiosus* | 2 | Z | Z | I | S1 | FALSE | FALSE |
| Muraenidae | *Gymnomuraena zebra* | 2 | MI | S | I | R | FALSE | TRUE |
| Muraenidae | *Gymnothorax eurostus* | 5 | MI | S | I | R | FALSE | FALSE |
| Muraenidae | *Gymnothorax flavimarginatus* | 2 | P | P | I | R | FALSE | FALSE |
| Muraenidae | *Gymnothorax javanicus* | 2 | P | S | I | R | FALSE | FALSE |
| Muraenidae | *Gymnothorax melatremus* | 2 | MI | S | I | R | FALSE | FALSE |
| Muraenidae | *Gymnothorax meleagris* | 2 | P | P | I | R | FALSE | FALSE |
| Muraenidae | *Gymnothorax nudivomer* | 2 | P | P | I | R | FALSE | FALSE |
| Muraenidae | *Gymnothorax pictus* | 2 | P | S | I | R | FALSE | FALSE |
| Muraenidae | *Gymnothorax rueppelliae* | 2 | MI | S | I | R | FALSE | FALSE |
| Muraenidae | *Gymnothorax species* | 2 | P | P | I | R | FALSE | FALSE |
| Muraenidae | *Gymnothorax steindachneri* | 8 | P | P | E | R | FALSE | FALSE |
| Muraenidae | *Gymnothorax undulatus* | 2 | P | P | I | R | FALSE | FALSE |
| Labridae | *Halichoeres ornatissimus* | 2 | MI | S | I | S1 | FALSE | TRUE |
| Hemiramphidae | *Hemiramphus depauperatus* | 6 | Hother | H | I | T | FALSE | FALSE |

| Family | Species | Zoogeog | Trophic 9 | Trophic 5 | Endemic | Mobility | Resource Species | HarvestedSpecies |
|---|---|---|---|---|---|---|---|---|
| Hemiramphidae | *Hemiramphus species* | 6 | Hother | H | I | T | FALSE | FALSE |
| Chaetodontidae | *Hemitaurichthys polylepis* | 2 | Z | Z | I | S1 | FALSE | FALSE |
| Chaetodontidae | *Hemitaurichthys thompsoni* | 5 | Z | Z | I | S1 | FALSE | FALSE |
| Chaetodontidae | *Heniochus diphreutes* | 2 | Z | Z | I | S1 | FALSE | FALSE |
| Priacanthidae | *Heteropriacanthus cruentatus* | 1 | Z | Z | I | R | TRUE | TRUE |
| Syngnathidae | *Hippocampus fisheri* | 8 | Z | Z | I | S1 | FALSE | FALSE |
| Syngnathidae | *Hippocampus kuda* | 2 | Z | Z | I | S1 | FALSE | FALSE |
| Holocentridae | *Holocentridae species* | 2 | MI | S | I | R | TRUE | TRUE |
| Hemiramphidae | *Hyporhamphus acutus* | 6 | Hother | H | I | T | FALSE | FALSE |
| Labridae | *Iniistius aneitensis* | 2 | MI | S | I | R | TRUE | TRUE |
| Labridae | *Iniistius baldwini* | 4 | MI | S | I | R | TRUE | TRUE |
| Labridae | *Iniistius niveilatus* | 2 | MI | S | I | R | TRUE | TRUE |
| Labridae | *Iniistius pavo* | 2 | MI | S | I | R | TRUE | TRUE |
| Labridae | *Iniistius species* | 2 | MI | S | I | R | TRUE | TRUE |
| Labridae | *Iniistius umbrilatus* | 8 | MI | S | E | R | TRUE | TRUE |
| Scorpaenidae | *Iracundus signifer* | 2 | MI | S | I | R | FALSE | FALSE |
| Blenniidae | *Istiblennius zebra* | 8 | Hother | H | E | R | FALSE | FALSE |
| Scombridae | *Katsuwonus pelamis* | 1 | P | APEX | I | T | TRUE | TRUE |
| Kuhliidae | *Kuhlia sandvicensis* | 6 | Z | Z | I | R | TRUE | TRUE |
| Kyphosidae | *Kyphosus bigibbus* | 5 | Hbrow | H | I | S2 | TRUE | TRUE |
| Kyphosidae | *Kyphosus cinerascens* | 2 | Hbrow | H | I | S2 | TRUE | TRUE |
| Kyphosidae | *Kyphosus hawaiiensis* | 8 | Hother | H | E | S2 | TRUE | TRUE |
| Kyphosidae | *Kyphosus sandwicensis* | 8 | Hother | H | E | S2 | TRUE | TRUE |
| Kyphosidae | *Kyphosus species* | 2 | Hother | H | I | S2 | TRUE | TRUE |
| Kyphosidae | *Kyphosus vaigiensis* | 2 | Hbrow | H | I | S2 | TRUE | TRUE |
| Labridae | *Labridae species* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Labridae | *Labroides phthirophagus* | 8 | P | S | E | R | FALSE | TRUE |
| Ostraciidae | *Lactoria fornasini* | 2 | SI | S | I | S1 | FALSE | FALSE |
| Lutjanidae | *Lutjanus fulvus* | 2 | MI | S | X | S1 | TRUE | TRUE |
| Lutjanidae | *Lutjanus kasmira* | 2 | MI | S | X | S2 | TRUE | TRUE |
| Labridae | *Macropharyngodon geoffroy* | 8 | MI | S | E | S1 | FALSE | FALSE |
| Malacanthidae | *Malacanthus brevirostris* | 2 | MI | S | I | S1 | FALSE | FALSE |

| Family | Species | Zoogeog | Trophic 9 | Trophic 5 | Endemic | Mobility | Resource Species | HarvestedSpecies |
|---|---|---|---|---|---|---|---|---|
| Mobulidae | *Manta alfredi* | 2 | Z | Z | I | T | FALSE | FALSE |
| Mobulidae | *Manta birostris* | 2 | Z | Z | I | T | FALSE | FALSE |
| Balistidae | *Melichthys niger* | 1 | Hother | H | I | S1 | FALSE | TRUE |
| Balistidae | *Melichthys vidua* | 2 | Hother | H | I | S1 | FALSE | TRUE |
| Scorpididae | *Microcanthus strigatus* | 5 | MI | S | I | S1 | TRUE | FALSE |
| Monacanthidae | *Monacanthidae species* | 2 | Hother | H | I | S1 | FALSE | FALSE |
| Lethrinidae | *Monotaxis grandoculis* | 2 | MI | S | I | S2 | TRUE | TRUE |
| Mugilidae | *Mugil cephalus* | 1 | D | S | I | T | TRUE | TRUE |
| Mullidae | *Mullidae species* | 2 | MI | S | I | S2 | TRUE | TRUE |
| Mullidae | *Mulloidichthys flavolineatus* | 2 | MI | S | I | S1 | TRUE | TRUE |
| Mullidae | *Mulloidichthys mimicus* | 6 | MI | S | I | S2 | TRUE | TRUE |
| Mullidae | *Mulloidichthys pflugeri* | 2 | P | P | I | S2 | TRUE | TRUE |
| Mullidae | *Mulloidichthys vanicolensis* | 2 | MI | S | I | S1 | TRUE | TRUE |
| Muraenidae | *Muraenidae species* | 2 | P | S | I | R | FALSE | FALSE |
| Ophichthidae | *Myrichthys magnificus* | 8 | MI | S | E | S1 | FALSE | FALSE |
| Holocentridae | *Myripristis amaena* | 6 | Z | Z | I | R | TRUE | TRUE |
| Holocentridae | *Myripristis berndti* | 2 | Z | Z | I | R | TRUE | TRUE |
| Holocentridae | *Myripristis chryseres* | 2 | Z | Z | I | R | TRUE | TRUE |
| Holocentridae | *Myripristis kuntee* | 2 | Z | Z | I | R | TRUE | TRUE |
| Holocentridae | *Myripristis species* | 2 | Z | Z | I | R | TRUE | TRUE |
| Holocentridae | *Myripristis vittata* | 2 | Z | Z | I | R | TRUE | TRUE |
| Acanthuridae | *Naso annulatus* | 2 | Z | Z | I | T | TRUE | TRUE |
| Acanthuridae | *Naso brevirostris* | 2 | Z | Z | I | T | TRUE | TRUE |
| Acanthuridae | *Naso caesius* | 2 | Z | Z | I | T | TRUE | TRUE |
| Acanthuridae | *Naso hexacanthus* | 2 | Z | Z | I | S1 | TRUE | TRUE |
| Acanthuridae | *Naso lituratus* | 2 | Hbrow | H | I | S2 | TRUE | TRUE |
| Acanthuridae | *Naso maculatus* | 5 | Z | Z | I | T | TRUE | FALSE |
| Acanthuridae | *Naso species* | 2 | Hother | H | I | S2 | TRUE | TRUE |
| Acanthuridae | *Naso unicornis* | 2 | Hbrow | H | I | S2 | TRUE | TRUE |
| Microdesmidae | *Nemateleotris magnifica* | 2 | Z | Z | I | S1 | FALSE | FALSE |
| Mugilidae | *Neomyxus leuciscus* | 6 | D | S | I | T | TRUE | TRUE |
| Holocentridae | *Neoniphon aurolineatus* | 2 | MI | S | I | S1 | TRUE | TRUE |

| Family | Species | Zoogeog | Trophic 9 | Trophic 5 | Endemic | Mobility | Resource Species | HarvestedSpecies |
|---|---|---|---|---|---|---|---|---|
| Holocentridae | *Neoniphon sammara* | 2 | MI | S | I | R | TRUE | TRUE |
| Holocentridae | *Neoniphon species* | 2 | MI | S | I | R | TRUE | TRUE |
| Labridae | *Novaculichthys taeniourus* | 2 | MI | S | I | S1 | FALSE | TRUE |
| Blenniidae | *Omobranchus rotundiceps* | 2 | Hother | H | I | R | FALSE | FALSE |
| Oplegnathidae | *Oplegnathus fasciatus* | 4 | MI | S | I | T | FALSE | FALSE |
| Oplegnathidae | *Oplegnathus punctatus* | 4 | MI | S | I | T | TRUE | TRUE |
| Gobiidae | *Opua nephodes* | 8 | Hother | H | I | S1 | FALSE | FALSE |
| Apogonidae | *Ostorhinchus maculiferus* | 8 | MI | S | E | R | FALSE | FALSE |
| Ostraciidae | *Ostracion meleagris* | 2 | SI | S | I | S1 | FALSE | TRUE |
| Ostraciidae | *Ostracion whitleyi* | 6 | SI | S | I | S1 | FALSE | FALSE |
| Labridae | *Oxycheilinus bimaculatus* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Labridae | *Oxycheilinus unifasciatus* | 2 | P | P | I | S1 | TRUE | TRUE |
| Cirrhitidae | *Oxycirrhites typus* | 2 | Z | Z | I | S1 | FALSE | FALSE |
| Blenniidae | *Parablennius thysanius* | 2 | Hother | H | X | R | FALSE | FALSE |
| Cirrhitidae | *Paracirrhites arcatus* | 2 | MI | S | I | R | FALSE | FALSE |
| Cirrhitidae | *Paracirrhites forsteri* | 2 | P | P | I | R | FALSE | FALSE |
| Pinguipedidae | *Parapercis schauinslandi* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Pinguipedidae | *Parapercis species* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Mullidae | *Parupeneus chrysonemus* | 8 | MI | S | E | S2 | TRUE | TRUE |
| Mullidae | *Parupeneus cyclostomus* | 2 | P | P | I | S2 | TRUE | TRUE |
| Mullidae | *Parupeneus insularis* | 3 | MI | S | I | S1 | TRUE | TRUE |
| Mullidae | *Parupeneus multifasciatus* | 2 | MI | S | I | S1 | TRUE | TRUE |
| Mullidae | *Parupeneus pleurostigma* | 2 | MI | S | I | S1 | TRUE | TRUE |
| Mullidae | *Parupeneus porphyreus* | 8 | MI | S | E | S1 | TRUE | TRUE |
| Monacanthidae | *Pervagor aspricaudus* | 2 | Hother | H | I | S1 | FALSE | FALSE |
| Monacanthidae | *Pervagor spilosoma* | 8 | Hother | H | E | S1 | FALSE | FALSE |
| Blenniidae | *Plagiotremus ewaensis* | 8 | P | P | E | R | FALSE | FALSE |
| Blenniidae | *Plagiotremus goslinei* | 8 | P | P | E | R | FALSE | FALSE |
| Belonidae | *Platybelone argalus* | 1 | P | P | I | T | FALSE | FALSE |
| Pomacentridae | *Plectroglyphidodon imparipennis* | 2 | MI | S | I | R | FALSE | FALSE |
| Pomacentridae | *Plectroglyphidodon johnstonianus* | 2 | C | S | I | R | FALSE | FALSE |

| Family | Species | Zoogeog | Trophic 9 | Trophic 5 | Endemic | Mobility | Resource Species | HarvestedSpecies |
|---|---|---|---|---|---|---|---|---|
| Pomacentridae | *Plectroglyphidodon sindonis* | 8 | Hother | H | E | R | FALSE | FALSE |
| Gobiidae | *Pleurosicya micheli* | 2 | C | S | I | R | FALSE | FALSE |
| Polynemidae | *Polydactylus sexfilis* | 2 | MI | S | I | S2 | TRUE | TRUE |
| Priacanthidae | *Priacanthus meeki* | 8 | Z | Z | E | R | TRUE | TRUE |
| Priacanthidae | *Priacanthus species* | 8 | Z | Z | I | R | TRUE | TRUE |
| Gobiidae | *Priolepis aureoviridis* | 6 | Hother | H | I | S1 | FALSE | FALSE |
| Gobiidae | *Priolepis eugenius* | 8 | SI | S | E | R | FALSE | FALSE |
| Apogonidae | *Pristiapogon kallopterus* | 2 | MI | S | I | R | FALSE | FALSE |
| Apogonidae | *Pristiapogon taeniopterus* | 2 | MI | S | I | R | FALSE | FALSE |
| Holocentridae | *Pristilepis oligolepis* | 5 | Z | Z | I | R | TRUE | FALSE |
| Anthias (Serranid) | *Pseudanthias bicolor* | 2 | Z | Z | I | S1 | FALSE | FALSE |
| Anthias (Serranid) | *Pseudanthias hawaiiensis* | 8 | Z | Z | E | S1 | FALSE | FALSE |
| Anthias (Serranid) | *Pseudanthias thompsoni* | 8 | Z | Z | E | S1 | FALSE | FALSE |
| Carangidae | *Pseudocaranx cheilio* | 8 | P | APEX | I | T | TRUE | TRUE |
| Labridae | *Pseudocheilinus evanidus* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Labridae | *Pseudocheilinus octotaenia* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Labridae | *Pseudocheilinus tetrataenia* | 5 | MI | S | I | S1 | FALSE | FALSE |
| Labridae | *Pseudojuloides cerasinus* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Gobiidae | *Psilogobius mainlandi* | 8 | SI | S | E | R | FALSE | FALSE |
| Microdesmidae | *Ptereleotris heteroptera* | 2 | Z | Z | I | S1 | FALSE | FALSE |
| Scorpaenidae | *Pterois sphex* | 8 | P | P | E | R | FALSE | FALSE |
| Balistidae | *Rhinecanthus aculeatus* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Balistidae | *Rhinecanthus rectangulus* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Holocentridae | *Sargocentron diadema* | 2 | MI | S | I | R | TRUE | TRUE |
| Holocentridae | *Sargocentron ensifer* | 5 | MI | S | I | R | TRUE | TRUE |
| Holocentridae | *Sargocentron punctatissimum* | 2 | MI | S | I | R | TRUE | TRUE |
| Holocentridae | *Sargocentron species* | 2 | MI | S | I | R | TRUE | TRUE |
| Holocentridae | *Sargocentron spiniferum* | 2 | MI | S | I | R | TRUE | TRUE |
| Holocentridae | *Sargocentron tiere* | 2 | MI | S | I | R | TRUE | TRUE |
| Holocentridae | *Sargocentron xantherythrum* | 8 | MI | S | E | R | TRUE | TRUE |
| Synodontidae | *Saurida flamma* | 5 | P | P | I | S2 | FALSE | FALSE |
| Synodontidae | *Saurida gracilis* | 2 | P | P | I | S2 | FALSE | FALSE |

| Family | Species | Zoogeog | Trophic 9 | Trophic 5 | Endemic | Mobility | Resource Species | HarvestedSpecies |
|---|---|---|---|---|---|---|---|---|
| Synodontidae | *Saurida species* | 2 | P | S | I | S2 | FALSE | FALSE |
| Scaridae | *Scarus dubius* | 8 | Hscex | H | E | S2 | TRUE | TRUE |
| Scaridae | *Scarus psittacus* | 2 | Hscex | H | I | S2 | TRUE | TRUE |
| Scaridae | *Scarus rubroviolaceus* | 2 | Hscex | H | I | S2 | TRUE | TRUE |
| Scaridae | *Scarus species* | 2 | Hother | H | I | S2 | TRUE | TRUE |
| Carangidae | *Scomberoides lysan* | 2 | P | APEX | I | T | TRUE | TRUE |
| Scorpaenidae | *Scorpaenodes kelloggi* | 2 | MI | S | I | R | FALSE | FALSE |
| Scorpaenidae | *Scorpaenodes parvipinnis* | 2 | MI | S | I | R | FALSE | FALSE |
| Scorpaenidae | *Scorpaenopsis brevifrons* | 8 | P | S | E | R | FALSE | FALSE |
| Scorpaenidae | *Scorpaenopsis cacopsis* | 8 | P | P | E | R | FALSE | FALSE |
| Scorpaenidae | *Scorpaenopsis diabolus* | 2 | P | P | I | R | FALSE | FALSE |
| Scorpaenidae | *Scorpaenopsis species* | 2 | P | S | I | R | FALSE | FALSE |
| Muraenidae | *Scuticaria okinawae* | 2 | P | S | I | R | FALSE | FALSE |
| Muraenidae | *Scuticaria tigrinus* | 2 | P | P | I | R | FALSE | FALSE |
| Scorpaenidae | *Sebastapistes ballieui* | 8 | MI | S | E | R | FALSE | FALSE |
| Scorpaenidae | *Sebastapistes coniorta* | 6 | MI | S | I | R | FALSE | FALSE |
| Scorpaenidae | *Sebastapistes species* | 6 | MI | S | I | R | FALSE | FALSE |
| Carangidae | *Selar crumenophthalmus* | 1 | Z | Z | I | T | TRUE | TRUE |
| Carangidae | *Seriola dumerili* | 1 | P | APEX | I | T | TRUE | TRUE |
| Carangidae | *Seriola rivoliana* | 1 | P | APEX | I | T | TRUE | TRUE |
| Sphyraenidae | *Sphyraena barracuda* | 1 | P | APEX | I | T | TRUE | TRUE |
| Sphyraenidae | *Sphyraena helleri* | 2 | P | APEX | I | T | TRUE | TRUE |
| Sphyrnidae | *Sphyrna lewini* | 1 | P | APEX | I | T | FALSE | FALSE |
| Clupeidae | *Spratelloides delicatulus* | 2 | Z | Z | I | T | FALSE | FALSE |
| Pomacentridae | *Stegastes marginatus* | 8 | Hother | H | I | R | FALSE | FALSE |
| Labridae | *Stethojulis balteata* | 8 | MI | S | E | S1 | FALSE | FALSE |
| Balistidae | *Sufflamen bursa* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Balistidae | *Sufflamen fraenatus* | 2 | MI | S | I | S2 | FALSE | FALSE |
| Syngnathidae | *Syngnathidae species* | 2 | Z | Z | I | S1 | FALSE | FALSE |
| Synodontidae | *Synodus binotatus* | 2 | P | P | I | S2 | FALSE | FALSE |
| Synodontidae | *Synodus dermatogenys* | 2 | P | P | I | S2 | FALSE | FALSE |
| Synodontidae | *Synodus lobeli* | 4 | P | P | I | S2 | FALSE | FALSE |

| Family | Species | Zoogeog | Trophic 9 | Trophic 5 | Endemic | Mobility | Resource Species | HarvestedSpecies |
|---|---|---|---|---|---|---|---|---|
| Synodontidae | *Synodus species* | 2 | P | P | I | S2 | FALSE | FALSE |
| Synodontidae | *Synodus ulae* | 4 | P | P | I | S2 | FALSE | FALSE |
| Synodontidae | *Synodus variegatus* | 2 | P | P | I | S2 | FALSE | FALSE |
| Synodontidae | *Synodontidae species* | 2 | P | S | I | S2 | FALSE | FALSE |
| Scorpaenidae | *Taenianotus triacanthus* | 2 | P | P | I | R | FALSE | FALSE |
| Tetraodontidae | *Tetraodontidae species* | 2 | Hother | S | I | S1 | FALSE | FALSE |
| Labridae | *Thalassoma ballieui* | 8 | MI | S | E | S2 | TRUE | TRUE |
| Labridae | *Thalassoma duperrey* | 8 | MI | S | E | S1 | FALSE | TRUE |
| Labridae | *Thalassoma lutescens* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Labridae | *Thalassoma purpureum* | 2 | MI | S | I | S1 | TRUE | TRUE |
| Labridae | *Thalassoma quinquevittatum* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Labridae | *Thalassoma species* | 2 | MI | S | I | S1 | FALSE | FALSE |
| Labridae | *Thalassoma trilobatum* | 2 | MI | S | I | S2 | FALSE | FALSE |
| Synodontidae | *Trachinocephalus myops* | 1 | P | P | I | S2 | FALSE | FALSE |
| Carcharhinidae | *Triaenodon obesus* | 2 | P | APEX | I | T | FALSE | FALSE |
| Gobiidae | *Trimma taylori* | 2 | SI | S | I | R | FALSE | FALSE |
| Belonidae | *Tylosurus crocodilus* | 1 | P | APEX | I | T | TRUE | TRUE |
| Mullidae | *Upeneus arge* | 2 | MI | S | I | S2 | TRUE | TRUE |
| Labridae | *Wetmorella albofasciata* | 2 | MI | S | I | R | FALSE | FALSE |
| Balistidae | *Xanthichthys auromarginatus* | 2 | Z | Z | I | S1 | FALSE | FALSE |
| Balistidae | *Xanthichthys mento* | 5 | Z | Z | I | S1 | FALSE | FALSE |
| Labridae | *Xyrichtys woodi* | 8 | MI | S | E | R | FALSE | FALSE |
| Zanclidae | *Zanclus cornutus* | 2 | SI | S | I | S1 | FALSE | TRUE |
| Acanthuridae | *Zebrasoma flavescens* | 2 | Hgd | H | I | S1 | FALSE | TRUE |
| Acanthuridae | *Zebrasoma veliferum* | 2 | Hgd | H | I | S1 | TRUE | TRUE |

Appendix II. Results of analysis of fish length and weight for 109 species.

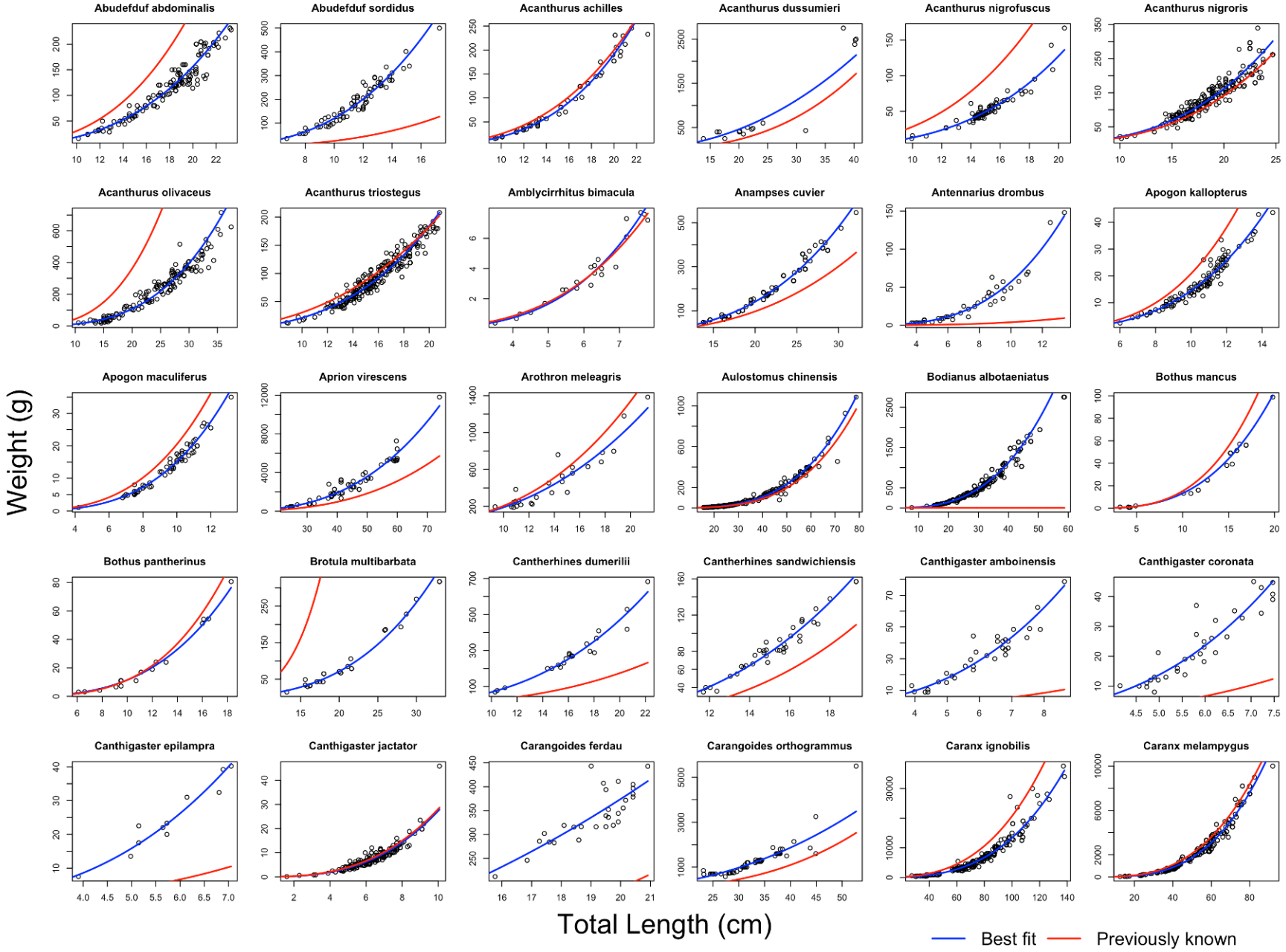
| Family | Species | N | log(*a*) | SE log(*a*) | SE *b* | $R^2$ | *p* | *a* | *b* |
|---|---|---|---|---|---|---|---|---|---|
| Pomacentridae | *Abudefduf abdominalis* | 147 | -4.061 | 0.169 | 0.058 | 0.95 | <0.001 | 0.017 | 3.039 |
| Pomacentridae | *Abudefduf sordidus* | 74 | -1.760 | 0.200 | 0.082 | 0.94 | <0.001 | 0.174 | 2.838 |
| Acanthuridae | *Acanthurus achilles* | 54 | -4.741 | 0.140 | 0.051 | 0.99 | <0.001 | 0.009 | 3.335 |
| Acanthuridae | *Acanthurus dussumieri* | 16 | -0.488 | 0.850 | 0.266 | 0.83 | <0.001 | 0.656 | 2.187 |
| Acanthuridae | *Acanthurus nigrofuscus* | 85 | -5.082 | 0.268 | 0.099 | 0.93 | <0.001 | 0.006 | 3.314 |
| Acanthuridae | *Acanthurus nigroris* | 234 | -3.757 | 0.184 | 0.063 | 0.90 | <0.001 | 0.024 | 2.948 |
| Acanthuridae | *Acanthurus olivaceus* | 151 | -4.966 | 0.207 | 0.066 | 0.94 | <0.001 | 0.007 | 3.211 |
| Acanthuridae | *Acanthurus triostegus* | 231 | -4.084 | 0.147 | 0.053 | 0.94 | <0.001 | 0.017 | 3.102 |
| Cirrhitidae | *Amblycirrhitus bimacula* | 22 | -5.281 | 0.238 | 0.133 | 0.97 | <0.001 | 0.005 | 3.593 |
| Labridae | *Anampses cuvier* | 161 | -4.112 | 0.096 | 0.032 | 0.98 | <0.001 | 0.016 | 3.024 |
| Antennariidae | *Antennarius drombus* | 44 | -3.280 | 0.198 | 0.102 | 0.96 | <0.001 | 0.039 | 3.168 |
| Apogonidae | *Apogon kallopterus* | 114 | -4.630 | 0.153 | 0.065 | 0.95 | <0.001 | 0.010 | 3.168 |
| Apogonidae | *Apogon maculiferus* | 66 | -4.828 | 0.140 | 0.063 | 0.98 | <0.001 | 0.008 | 3.274 |
| Lutjanidae | *Aprion virescens* | 75 | -2.918 | 0.281 | 0.075 | 0.95 | <0.001 | 0.055 | 2.834 |
| Tetraodontidae | *Arothron meleagris* | 27 | -0.546 | 0.498 | 0.191 | 0.87 | <0.001 | 0.593 | 2.505 |
| Aulostomidae | *Aulostomus chinensis* | 230 | -7.936 | 0.089 | 0.025 | 0.99 | <0.001 | 0.000 | 3.417 |
| Labridae | *Bodianus albotaeniatus* | 464 | -3.883 | 0.053 | 0.016 | 0.99 | <0.001 | 0.021 | 2.955 |
| Bothidae | *Bothus mancus* | 31 | -4.301 | 0.235 | 0.093 | 0.97 | <0.001 | 0.014 | 2.974 |
| Bothidae | *Bothus pantherinus* | 18 | -4.791 | 0.298 | 0.124 | 0.98 | <0.001 | 0.008 | 3.135 |
| Ophidiidae | *Brotula multibarbata* | 29 | -5.270 | 0.337 | 0.112 | 0.97 | <0.001 | 0.005 | 3.181 |
| Monacanthidae | *Cantherhines dumerilii* | 22 | -2.149 | 0.266 | 0.096 | 0.98 | <0.001 | 0.117 | 2.770 |
| Monacanthidae | *Cantherhines sandwichiensis* | 38 | -3.600 | 0.310 | 0.114 | 0.95 | <0.001 | 0.027 | 2.940 |
| Tetraodontidae | *Canthigaster amboinensis* | 33 | -1.418 | 0.280 | 0.156 | 0.90 | <0.001 | 0.246 | 2.660 |
| Tetraodontidae | *Canthigaster coronata* | 33 | -2.145 | 0.399 | 0.227 | 0.85 | <0.001 | 0.120 | 2.950 |
| Tetraodontidae | *Canthigaster epilampra* | 11 | -1.668 | 0.409 | 0.235 | 0.94 | <0.001 | 0.190 | 2.749 |
| Tetraodontidae | *Canthigaster jactator* | 185 | -3.379 | 0.102 | 0.055 | 0.94 | <0.001 | 0.035 | 2.898 |
| Carangidae | *Carangoides ferdau* | 29 | -0.470 | 0.753 | 0.255 | 0.72 | <0.001 | 0.627 | 2.133 |
| Carangidae | *Carangoides orthogrammus* | 59 | -0.797 | 0.389 | 0.112 | 0.88 | <0.001 | 0.456 | 2.255 |
| Carangidae | *Caranx ignobilis* | 229 | -4.673 | 0.156 | 0.037 | 0.97 | <0.001 | 0.009 | 3.075 |
| Carangidae | *Caranx melampygus* | 265 | -4.807 | 0.089 | 0.023 | 0.99 | <0.001 | 0.008 | 3.135 |
| Pomacanthidae | *Centropyge potteri* | 62 | -2.565 | 0.311 | 0.136 | 0.86 | <0.001 | 0.078 | 2.622 |
| Serranidae | *Cephalopholis argus* | 1201 | -4.464 | 0.063 | 0.018 | 0.96 | <0.001 | 0.012 | 3.140 |

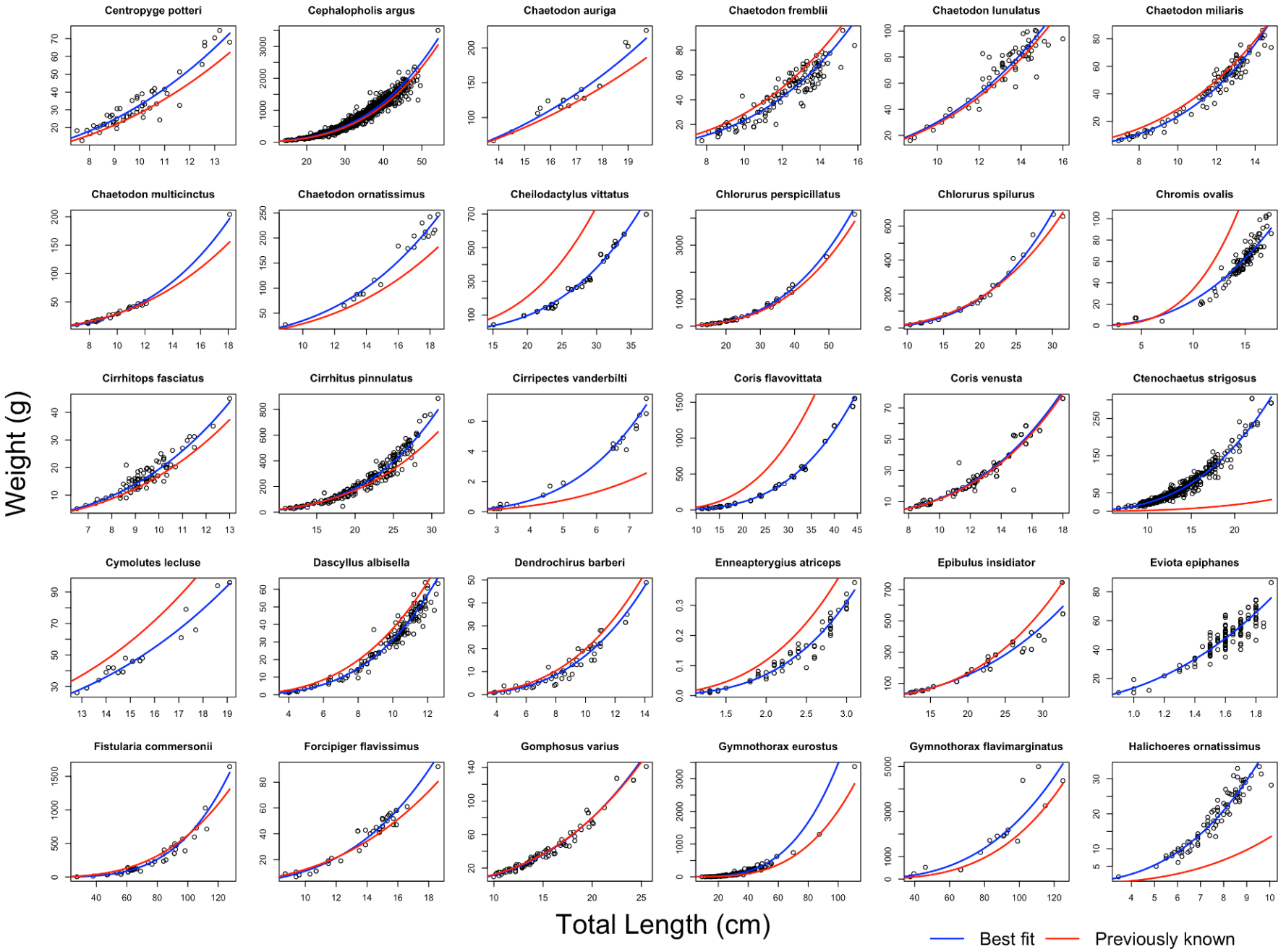
| Family | Species | N | log(*a*) | SE log(*a*) | SE *b* | $R^2$ | *p* | *a* | *b* |
|---|---|---|---|---|---|---|---|---|---|
| Chaetodontidae | *Chaetodon auriga* | 23 | -4.052 | 0.503 | 0.179 | 0.94 | <0.001 | 0.017 | 3.159 |
| Chaetodontidae | *Chaetodon fremblii* | 128 | -4.279 | 0.264 | 0.106 | 0.88 | <0.001 | 0.014 | 3.221 |
| Chaetodontidae | *Chaetodon lunulatus* | 66 | -3.452 | 0.337 | 0.131 | 0.89 | <0.001 | 0.032 | 2.977 |
| Chaetodontidae | *Chaetodon miliaris* | 98 | -4.895 | 0.160 | 0.065 | 0.97 | <0.001 | 0.008 | 3.495 |
| Chaetodontidae | *Chaetodon multicinctus* | 31 | -4.073 | 0.158 | 0.069 | 0.99 | <0.001 | 0.017 | 3.230 |
| Chaetodontidae | *Chaetodon ornatissimus* | 20 | -3.688 | 0.310 | 0.113 | 0.98 | <0.001 | 0.025 | 3.144 |
| Scaridae | *Chlorurus perspicillatus* | 51 | -3.928 | 0.111 | 0.034 | 0.99 | <0.001 | 0.020 | 3.039 |
| Scaridae | *Chlorurus spilurus* | 33 | -4.888 | 0.143 | 0.050 | 0.99 | <0.001 | 0.008 | 3.352 |
| Pomacentridae | *Chromis ovalis* | 116 | -2.409 | 0.177 | 0.066 | 0.92 | <0.001 | 0.091 | 2.413 |
| Cirrhitidae | *Cirrhitops fasciatus* | 101 | -4.158 | 0.271 | 0.122 | 0.87 | <0.001 | 0.016 | 3.090 |
| Cirrhitidae | *Cirrhitus pinnulatus* | 273 | -4.851 | 0.131 | 0.043 | 0.96 | <0.001 | 0.008 | 3.361 |
| Blenniidae | *Cirripectes vanderbilti* | 22 | -5.236 | 0.210 | 0.126 | 0.98 | <0.001 | 0.005 | 3.559 |
| Labridae | *Coris flavovittata* | 296 | -5.338 | 0.031 | 0.009 | 1.00 | <0.001 | 0.005 | 3.347 |
| Labridae | *Coris venusta* | 225 | -4.993 | 0.122 | 0.048 | 0.95 | <0.001 | 0.007 | 3.245 |
| Acanthuridae | *Ctenochaetus strigosus* | 442 | -3.646 | 0.080 | 0.031 | 0.95 | <0.001 | 0.026 | 2.939 |
| Labridae | *Cymolutes lecluse* | 24 | -4.676 | 0.353 | 0.129 | 0.96 | <0.001 | 0.009 | 3.129 |
| Pomacentridae | *Dascyllus albisella* | 170 | -4.129 | 0.079 | 0.035 | 0.98 | <0.001 | 0.016 | 3.284 |
| Scorpaenidae | *Dendrochirus barberi* | 55 | -4.200 | 0.275 | 0.129 | 0.91 | <0.001 | 0.016 | 3.037 |
| Tripterygiidae | *Enneapterygius atriceps* | 58 | -5.203 | 0.082 | 0.096 | 0.96 | <0.001 | 0.006 | 3.659 |
| Labridae | *Epibulus insidiator* | 61 | -3.157 | 0.184 | 0.060 | 0.97 | <0.001 | 0.043 | 2.733 |
| Gobiidae | *Eviota epiphanes* | 144 | 2.591 | 0.043 | 0.091 | 0.86 | <0.001 | 0.135 | 2.692 |
| Fistulariidae | *Fistularia commersonii* | 51 | -11.122 | 0.489 | 0.115 | 0.96 | <0.001 | 0.000 | 3.804 |
| Chaetodontidae | *Forcipiger flavissimus* | 60 | -5.742 | 0.276 | 0.105 | 0.95 | <0.001 | 0.003 | 3.538 |
| Labridae | *Gomphosus varius* | 92 | -3.967 | 0.131 | 0.048 | 0.97 | <0.001 | 0.019 | 2.785 |
| Cheilodactylidae | *Goniistius vittatus* | 368 | -5.498 | 0.131 | 0.048 | 0.99 | <0.001 | 0.004 | 3.363 |
| Muraenidae | *Gymnothorax eurostus* | 138 | -6.970 | 0.167 | 0.049 | 0.97 | <0.001 | 0.001 | 3.277 |
| Muraenidae | *Gymnothorax flavimarginatus* | 18 | -5.738 | 1.175 | 0.268 | 0.88 | <0.001 | 0.003 | 2.941 |
| Labridae | *Halichoeres ornatissimus* | 83 | -3.024 | 0.168 | 0.083 | 0.94 | <0.001 | 0.049 | 2.914 |
| Priacanthidae | *Heteropriacanthus cruentatus* | 32 | -3.886 | 0.245 | 0.078 | 0.98 | <0.001 | 0.021 | 2.897 |
| Labridae | *Iniistius pavo* | 137 | -0.611 | 0.355 | 0.115 | 0.72 | <0.001 | 0.556 | 2.165 |
| Kyphosidae | *Kyphosus bigibbus* | 42 | -5.431 | 0.368 | 0.110 | 0.96 | <0.001 | 0.004 | 3.405 |
| Lutjanidae | *Lutjanus kasmira* | 273 | -4.194 | 0.119 | 0.040 | 0.95 | <0.001 | 0.015 | 2.985 |
| Labridae | *Macropharyngodon geoffroy* | 43 | -3.958 | 0.223 | 0.093 | 0.96 | <0.001 | 0.019 | 3.015 |

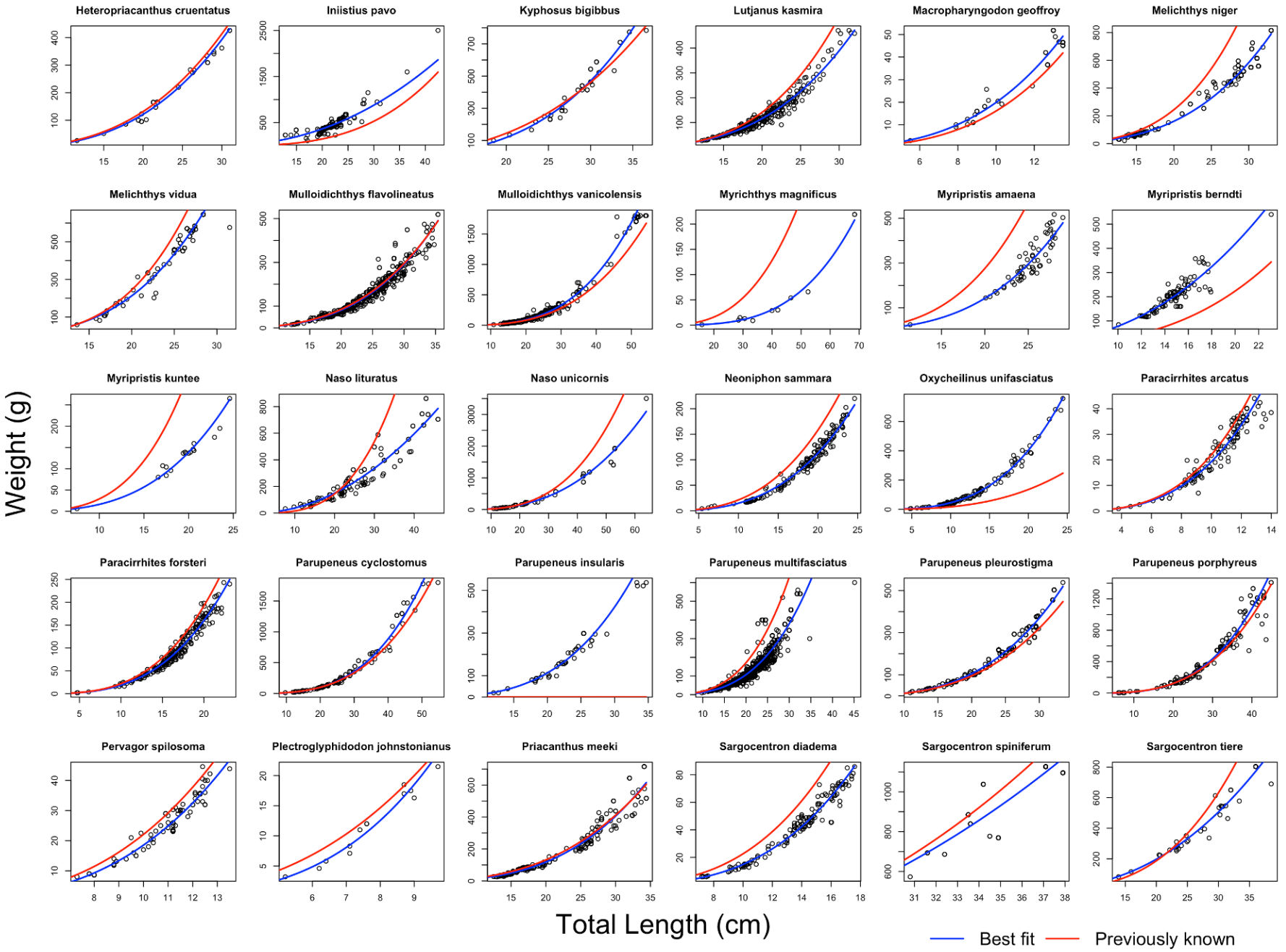
| Family | Species | N | log(*a*) | SE log(*a*) | SE *b* | $R^2$ | *p* | *a* | *b* |
|---|---|---|---|---|---|---|---|---|---|
| Balistidae | *Melichthys niger* | 149 | -4.439 | 0.115 | 0.036 | 0.98 | <0.001 | 0.012 | 3.175 |
| Balistidae | *Melichthys vidua* | 107 | -4.242 | 0.204 | 0.064 | 0.96 | <0.001 | 0.014 | 3.203 |
| Mullidae | *Mulloidichthys flavolineatus* | 762 | -5.033 | 0.071 | 0.022 | 0.96 | <0.001 | 0.007 | 3.146 |
| Mullidae | *Mulloidichthys vanicolensis* | 556 | -5.088 | 0.063 | 0.020 | 0.98 | <0.001 | 0.006 | 3.199 |
| Ophichthidae | *Myrichthys magnificus* | 11 | -9.796 | 0.719 | 0.196 | 0.97 | <0.001 | 0.000 | 3.573 |
| Holocentridae | *Myripristis amaena* | 58 | -4.859 | 0.415 | 0.129 | 0.92 | <0.001 | 0.008 | 3.274 |
| Holocentridae | *Myripristis berndti* | 96 | -1.206 | 0.305 | 0.113 | 0.83 | <0.001 | 0.302 | 2.415 |
| Holocentridae | *Myripristis kuntee* | 17 | -4.342 | 0.300 | 0.102 | 0.98 | <0.001 | 0.013 | 3.093 |
| Acanthuridae | *Naso lituratus* | 105 | -0.974 | 0.184 | 0.057 | 0.92 | <0.001 | 0.386 | 1.990 |
| Acanthuridae | *Naso unicornis* | 67 | -2.927 | 0.100 | 0.031 | 0.99 | <0.001 | 0.054 | 2.635 |
| Holocentridae | *Neoniphon sammara* | 188 | -4.040 | 0.099 | 0.034 | 0.97 | <0.001 | 0.018 | 2.924 |
| Labridae | *Oxycheilinus unifasciatus* | 110 | -3.494 | 0.080 | 0.032 | 0.99 | <0.001 | 0.031 | 3.167 |
| Cirrhitidae | *Paracirrhites arcatus* | 106 | -4.100 | 0.171 | 0.073 | 0.94 | <0.001 | 0.017 | 3.060 |
| Cirrhitidae | *Paracirrhites forsteri* | 220 | -4.190 | 0.085 | 0.031 | 0.98 | <0.001 | 0.015 | 3.091 |
| Mullidae | *Parupeneus cyclostomus* | 129 | -4.881 | 0.080 | 0.025 | 0.99 | <0.001 | 0.008 | 3.160 |
| Mullidae | *Parupeneus insularis* | 59 | -5.009 | 0.246 | 0.079 | 0.97 | <0.001 | 0.007 | 3.247 |
| Mullidae | *Parupeneus multifasciatus* | 983 | -4.690 | 0.076 | 0.025 | 0.94 | <0.001 | 0.009 | 3.121 |
| Mullidae | *Parupeneus pleurostigma* | 350 | -4.596 | 0.053 | 0.017 | 0.99 | <0.001 | 0.010 | 3.088 |
| Mullidae | *Parupeneus porphyreus* | 181 | -4.625 | 0.094 | 0.028 | 0.99 | <0.001 | 0.010 | 3.143 |
| Monacanthidae | *Pervagor spilosoma* | 96 | -4.198 | 0.169 | 0.071 | 0.95 | <0.001 | 0.015 | 3.089 |
| Pomacentridae | *Plectroglyphidodon johnstonianus* | 13 | -4.328 | 0.384 | 0.189 | 0.96 | <0.001 | 0.013 | 3.295 |
| Priacanthidae | *Priacanthus meeki* | 225 | -4.359 | 0.092 | 0.030 | 0.98 | <0.001 | 0.013 | 3.045 |
| Holocentridae | *Sargocentron diadema* | 169 | -4.455 | 0.089 | 0.034 | 0.98 | <0.001 | 0.012 | 3.106 |
| Holocentridae | *Sargocentron spiniferum* | 73 | -3.303 | 0.548 | 0.154 | 0.83 | <0.001 | 0.037 | 2.851 |
| Holocentridae | *Sargocentron tiere* | 38 | -1.672 | 0.241 | 0.072 | 0.97 | <0.001 | 0.189 | 2.321 |
| Holocentridae | *Sargocentron xantherythrum* | 64 | -3.850 | 0.289 | 0.116 | 0.91 | <0.001 | 0.021 | 2.904 |
| Synodontidae | *Saurida gracilis* | 138 | -5.110 | 0.145 | 0.050 | 0.97 | <0.001 | 0.006 | 3.122 |
| Scaridae | *Scarus dubius* | 40 | -4.154 | 0.171 | 0.059 | 0.99 | <0.001 | 0.016 | 3.097 |
| Scorpaenidae | *Scorpaenodes kelloggi* | 28 | -4.530 | 0.228 | 0.202 | 0.91 | <0.001 | 0.011 | 3.256 |
| Scorpaenidae | *Scorpaenopsis cacopsis* | 31 | -4.176 | 0.073 | 0.025 | 1.00 | <0.001 | 0.015 | 3.136 |
| Scorpaenidae | *Scorpaenopsis diabolus* | 101 | -4.437 | 0.171 | 0.060 | 0.97 | <0.001 | 0.012 | 3.321 |
| Scorpaenidae | *Sebastapistes ballieui* | 154 | -4.694 | 0.134 | 0.067 | 0.94 | <0.001 | 0.009 | 3.418 |
| Scorpaenidae | *Sebastapistes coniorta* | 49 | -3.984 | 0.189 | 0.099 | 0.95 | <0.001 | 0.019 | 3.115 |

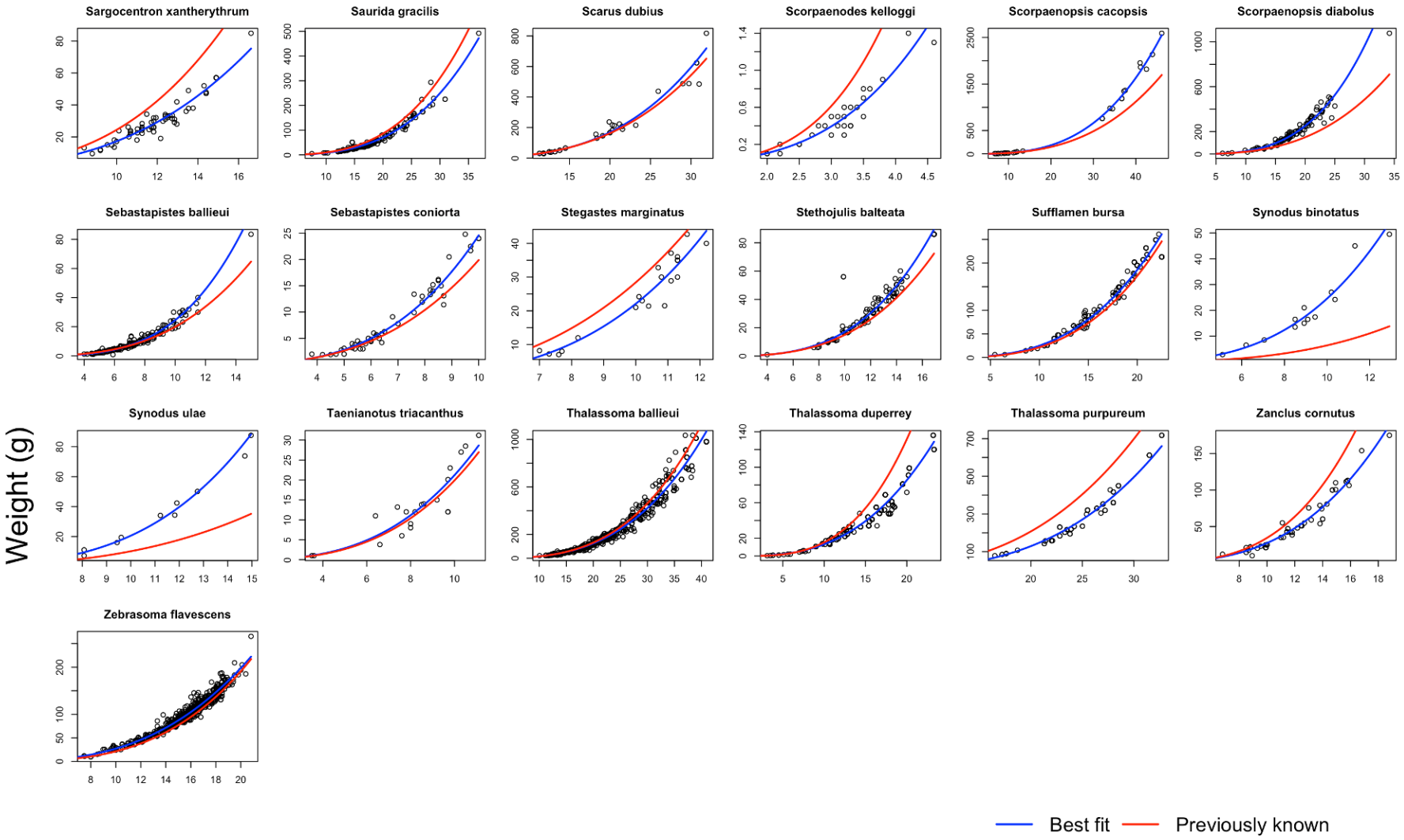
| Family | Species | N | log(*a*) | SE log(*a*) | SE *b* | $R^2$ | *p* | *a* | *b* |
|---|---|---|---|---|---|---|---|---|---|
| Pomacentridae | *Stegastes marginatus* | 20 | -4.815 | 0.436 | 0.189 | 0.95 | <0.001 | 0.008 | 3.431 |
| Labridae | *Stethojulis balteata* | 148 | -4.430 | 0.163 | 0.066 | 0.94 | <0.001 | 0.012 | 3.152 |
| Balistidae | *Sufflamen bursa* | 166 | -3.449 | 0.089 | 0.032 | 0.98 | <0.001 | 0.032 | 2.893 |
| Synodontidae | *Synodus binotatus* | 13 | -3.879 | 0.361 | 0.166 | 0.97 | <0.001 | 0.021 | 3.071 |
| Synodontidae | *Synodus ulae* | 10 | -5.311 | 0.491 | 0.204 | 0.98 | <0.001 | 0.005 | 3.616 |
| Scorpaenidae | *Taenianotus triacanthus* | 20 | -3.625 | 0.479 | 0.230 | 0.90 | <0.001 | 0.028 | 2.880 |
| Labridae | *Thalassoma ballieui* | 836 | -4.140 | 0.037 | 0.012 | 0.99 | <0.001 | 0.016 | 2.993 |
| Labridae | *Thalassoma duperrey* | 367 | -3.631 | 0.068 | 0.026 | 0.97 | <0.001 | 0.027 | 2.693 |
| Labridae | *Thalassoma purpureum* | 66 | -5.106 | 0.210 | 0.065 | 0.98 | <0.001 | 0.006 | 3.325 |
| Zanclidae | *Zanclus cornutus* | 55 | -3.751 | 0.253 | 0.102 | 0.94 | <0.001 | 0.024 | 3.060 |
| Acanthuridae | *Zebrasoma flavescens* | 556 | -3.282 | 0.058 | 0.021 | 0.97 | <0.001 | 0.038 | 2.860 |

Appendix III.




Centropyge potteri
Cephalopholis argus
Chaetodon auriga
Chaetodon fremblii
Chaetodon lunulatus
Chaetodon miliaris
Chaetodon multicinctus
Chaetodon ornatissimus
Cheilodactylus vittatus
Chlorurus perspicillatus
Chlorurus spilurus
Chromis ovalis
Cirrhitops fasciatus
Cirrhitus pinnulatus
Cirripectes vanderbilti
Coris flavovittata
Coris venusta
Ctenochaetus strigosus
Cymolutes lecluse
Dascyllus albisella
Dendrochirus barberi
Enneapterygius atriceps
Epibulus insidiator
Eviota epiphanes
Fistularia commersonii
Forcipiger flavissimus
Gomphosus varius
Gymnothorax eurostus
Gymnothorax flavimarginatus
Halichoeres ornatissimus
Weight (g)
Total Length (cm)
Best fit
Previously known


Heteropriacanthus cruentatus
Iniistius pavo
Kyphosus bigibbus
Lutjanus kasmira
Macropharyngodon geoffroy
Melichthys niger
Melichthys vidua
Mulloidichthys flavolineatus
Mulloidichthys vanicolensis
Myrichthys magnificus
Myripristis amaena
Myripristis berndti
Myripristis kuntee
Naso lituratus
Naso unicornis
Neoniphon sammara
Oxycheilinus unifasciatus
Paracirrhites arcatus
Paracirrhites forsteri
Parupeneus cyclostomus
Parupeneus insularis
Parupeneus multifasciatus
Parupeneus pleurostigma
Parupeneus porphyreus
Pervagor spilosoma
Plectroglyphidodon johnstonianus
Priacanthus meeki
Sargocentron diadema
Sargocentron spiniferum
Sargocentron tiere
Weight (g)
Total Length (cm)
Best fit
Previously known


Sargocentron xantherythrum
Saurida gracilis
Scarus dubius
Scorpaenodes kelloggi
Scorpaenopsis cacopsis
Scorpaenopsis diabolus
Sebastapistes ballieui
Sebastapistes coniorta
Stegastes marginatus
Stethojulis balteata
Sufflamen bursa
Synodus binotatus
Synodus ulae
Taenianotus triacanthus
Thalassoma ballieui
Thalassoma duperrey
Thalassoma purpureum
Zanclus cornutus
Zebrasoma flavescens
Weight (g)
Best fit
Previously known
Total Length (cm)