Vol. 597: 221–230, 2018
https://doi.org/10.3354/meps12593

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published June 11

From migrants to mossbacks: tracer- and tag-inferred habitat shifts in the California yellowtail *Seriola dorsalis*

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ABSTRACT: The California yellowtail *Seriola dorsalis* (YT) is an economically and ecologically valuable predator in both coastal and pelagic regions of the California Current Ecosystem. Delineating size-structured migration patterns can help assess population connectivity and predict effects of regional fishing pressure. We used chemical tracers (stable isotope analysis and mercury analysis) and conventional tagging to evaluate the dynamics of a potential ontogenetic shift in habitat from pelagic waters to coastal regions. Stable isotope analysis revealed a shift in habitat use at intermediate sizes (fork length, FL = 76 to 87.5 cm). Smaller YT were isotopically similar to pelagic yellowfin tuna *Thunnus albacares*, while larger YT were isotopically similar to the coastal white seabass *Atractoscion nobilis*. Tag recaptures from a small number of fish (48 deployments, 15 recaptures) corroborated an ontogenetic shift from offshore to coastal habitats, suggesting local, residential populations of larger YT in nearshore areas. Mercury concentrations increased directly after the observed habitat shift (FL = 88.3 cm), which is likely a result of both bioaccumulation with age and a shift to higher Hg prey inshore. Residential behavior of mature YT > 80 cm (~4 to 12+ yr old) suggests that regional size distributions could be influenced by local fishing pressure and inshore movement dynamics, as recruitment of migrants from southern waters will likely be comprised of smaller, younger fish.

KEY WORDS: Stable isotope · Pacific Ocean · Ontogenetic · Fish · Tagging · Mercury · Carbon-13 · Nitrogen-15

INTRODUCTION

Ontogenetic shifts in habitat are common in marine fish. The evolutionary underpinnings for these behaviors may vary by species or phylogenetic groupings, but are generally attributed to reduction in predation risk, access to potential settlement habitat, and optimal food resources for juveniles (Werner & Gilliam 1984, Grol et al. 2014). Many large reef teleosts (e.g. groupers, snappers) have a larval pelagic stage followed by 'settling' into a residential role on reefs (Dahlgren & Eggleston 2000), while some coastal species (e.g. white seabass *Atractoscion nobilis*, weakfish *Cynoscion regalis*, striped bass *Morone saxatilis*) have a juvenile phase in coastal and/or estuarine systems before becoming more migratory and oceanic (Deegan 1993, Allen et al. 2007). Life history studies continue to reveal the complexity of predator movements and habitat utilization, and understanding these shifts throughout the ontogeny of marine predators facilitates sound management and clarifies the ecological impacts of these predators on multiple ecosystems (McCauley et al. 2012).

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The California yellowtail *Seriola dorsalis* (YT) is found in both coastal and pelagic regions of the southern California Current Ecosystem (CCE), as far north as the Channel Islands of California, USA, and as far south as the southern end of Baja California, Mexico. YT are high trophic-level predators that consume primarily teleosts (e.g. sardine *Sardinops sagax*, anchovy *Engraulis mordax*, Pacific and jack mackerels *Scomber japonicus* and *Trachurus symmetricus*, rockfish *Sebastes* spp., topsmelt *Atherinops affinis*, herring *Clupea pallasii*), market squid *Doryteuthis opalescens*, and pelagic red crab *Pleuroncodes planipes* (Baxter 1960). Size differences between individuals captured and observed in nearshore versus offshore waters, as well as historical tag–recapture data (Baxter 1960) suggest an ontogenetic habitat shift in the CCE. Large numbers of smaller fish ('migrants') are observed in pelagic waters, while larger fish are thought to be coastal residents ('mossbacks') (Baxter 1960). However, the life history stages associated with this habitat shift in the contemporary CCE, and associated foraging ecology across habitats, have not been investigated in present-day YT populations.

Tagging studies have long been used to estimate population size, mortality, and large-scale movements of fish (Pollock 1991, Kohler & Turner 2001, Pine et al. 2003). Conventional tags provide capture and recapture location data as well as time-at-liberty data, allowing measurement of net movement rates. While tagging studies provide insight into where fish go post-tagging, they cannot provide movement information retrospective from the time of tagging. Stable isotope analysis (SIA) is a more recent tool used to retrospectively assess time-integrated estimates of foraging ecology and/or movement patterns (Hobson 1999, Post 2002, Phillips & Eldridge 2006, Madigan et al. 2014). Stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) have been used to describe habitat use in predators that move between isotopically distinct ecoregions (Dale et al. 2011, Madigan et al. 2014, Carlisle et al. 2015). Mercury (Hg) concentrations can also lend insight into predator ecology and movements, based on trophic bioaccumulation and differences in Hg concentrations across habitats (Julshamn et al. 1982, Power et al. 2002). Tagging studies and chemical tracer approaches are particularly powerful in combination, gathering prospective and retrospective movement and feeding information from both live and harvested animals (Cunjak et al. 2005, Carlisle et al. 2012, Madigan et al. 2015a). This combined approach allows for habitat shifts and ecosystem-specific feeding ecology to be comprehensively assessed.

We used SIA of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) to determine the extent to which YT captured both inshore and offshore reflect the prey and predator signatures from their capture areas. We combined SIA, conventional tagging, and Hg analyses to ascertain the size(s) over which the potential shift from pelagic to coastal waters takes place, and to link habitat shift to associated foraging patterns in both YT habitats.

MATERIALS AND METHODS

Sampling, SIA, and Hg

YT were captured by hook-and-line in the Southern California Bight (SCB) or sampled from fish captured by recreational anglers fishing near San Diego, CA. All fish sampled from recreational anglers were captured ≤200 km from the landing port of San Diego. For all whole individual fish, fork length (FL; cm) was measured and recorded. When the whole fish was not available, operculum length (OL, length from tip of the snout to the outer edge of the operculum; cm) was measured. FL was estimated from OL using an equation calculated by the authors from YT measurements ($n = 74$, $r^2 = 0.98$), as part of the National Oceanic and Atmospheric Administration Southwest Fisheries Science Center's (NOAA SWFSC) fish sampling program:

$$FL = 4.0869 \times OL - 0.0459 \quad (1)$$

White muscle (WM) tissue was taken from the dorsal musculature ~2 cm below the skin and immediately frozen at −5°C. YT were targeted and caught either offshore (pelagic waters, typically defined here by breaks in water clarity, temperature, and color from inshore waters; often near small drifting kelp mats of *Macrocystis* spp.) or inshore (coastal, usually around anchored kelp beds), and were initially categorized ('inshore' or 'offshore') according to capture location. To compare YT SIA values to similarly sized teleost predators from both pelagic and coastal habitats in the CCE, we collected WM tissue from yellowfin tuna and white seabass. These species are, respectively, pelagic and coastal in the CCE (Schaefer et al. 2007, Williams et al. 2007). WM was sampled from yellowfin and white seabass as described above for YT. Forage fish, cephalopods, and crustaceans that are known YT prey were sampled from the pelagic and coastal CCE. For forage fish, WM was sampled from the dorsal musculature just below the skin. For squids, a section of mantle tissue

was taken. For crustaceans (pelagic red crab), muscle was removed from the tail section.

For SIA, all tissue samples were frozen at –80°C for 24 h, lyophilized for 72 h, and homogenized using a Wig-L-Bug (Sigma Aldrich). Analyses of $\delta^{13}C$ and $\delta^{15}N$ were performed at the University of Hawaii using an on-line C-N analyzer coupled with a Delta XP isotope ratio mass spectrometer. Replicate reference materials of atmospheric nitrogen and V-PDB were analyzed between approximately 10 samples. Muscle $\delta^{13}C$ values were arithmetically corrected for lipid content when appropriate (C:N > 3.4) (Pinnegar & Polunin 1999, Logan et al. 2008), with the caveat that other studies suggest a different threshold of C:N >3.5 (Sweeting et al. 2006) based on C:N ratios and according to tissue-specific (e.g. fish muscle, squid muscle) correction algorithms in Logan et al. (2008). All SIA values are reported in ‰. For Hg analyses, tissue samples were lyophilized as above and homogenized using trace-metal-free techniques. Mercury concentration was measured in YT, white seabass, yellowfin tuna, and prey using a Milestone DMA-80 Direct Mercury Analyzer. A 1.0 ppm in-house Hg solution and DORM-4 standard were run with all samples to ensure proper DMA-80 calibration. All mercury concentrations are reported in µg g^{-1} dry weight (dw).

Statistical analyses

To assess ontogenetic changes in habitat use using SIA, we plotted YT size versus both $\delta^{13}C$ and $\delta^{15}N$ and performed segmented regression to evaluate the size at which YT isotopic signatures shift from those consistent with offshore habitat use to inshore habitat use. Segmented linear regression fits different linear functions to data, and defines breakpoints to maximize differences between slopes of multiple linear fits. To assess the degree to which individual YT reflect their region of capture (pelagic or inshore), we used discriminant analysis to group individual YT using yellowfin tuna (offshore) and white seabass (inshore) SIA values as training data. Individual YT were first grouped as inshore or offshore based on capture location; discriminant analysis then secondarily identified each individual as inshore or offshore based on SIA values.

We also performed segmented regression fits on YT Hg data to assess the size at which the Hg change was most substantial. Statistical significance of length and Hg measurements were assessed using Spearman's rho due to non-normality of data. Slopes of YT size versus Hg were compared to linear Hg slopes for similarly sized yellowfin tuna (pelagic) and white seabass (inshore) using analysis of covariance (ANCOVA). Hg concentrations were compared between inshore- and offshore-classified YT using the non-parametric Mann-Whitney *U*-test. All statistical analyses were carried out using MATLAB version R2017b.

Conventional tagging

Tagging equipment and instructions were provided to recreational anglers in southern California as part of a cooperative tagging effort through NOAA SWFSC. YT were captured via hook-and-line in both nearshore and pelagic regions on recreational fishing vessels. YT were brought on board, measured for FL, implanted with FIM-96 floy tags in the dorsal musculature, and released. Location data and date were recorded for all tag deployments. Contact information was printed on FIM-96 floy tags to obtain information on the date and location of YT recapture.

RESULTS

SIA and Hg

WM samples were collected from 72 YT between 2008 and 2011. Size ranged from 50.7 to 120.7 cm (mean ± SD, 84.2 ± 16.6 cm), with 45 fish caught in pelagic waters and 27 caught in coastal waters. WM was collected from 14 white seabass (WSB) and 109 yellowfin tuna (YFT). Prey samples included (inshore): sardine, Pacific mackerel, jack mackerel, topsmelt, market squid; and (offshore): sardine, juvenile Pacific mackerel, market squid, juvenile jack mackerel, juvenile rockfish, pelagic red crab, and Pacific saury *Cololabis saira* (Table 1, Fig. 1). Offshore and inshore prey and predators segregated well in $\delta^{13}C$ versus $\delta^{15}N$ isospace, with minimal overlap between groups (Fig. 1).

The size ranges of YT sampled inshore versus offshore were significantly different (Mann-Whitney *U*-test, $p < 0.01$), with larger YT inshore (83 to 121 cm; 9 ± 9 cm) than offshore (51 to 102 cm; 80 ± 14 cm). Segmented regression of YT size versus $\delta^{15}N$ and $\delta^{13}C$ showed overlapping periods of rapid isotopic change in muscle tissue: between 76 and 82.5 cm for $\delta^{15}N$ and between 80 and 87.5 cm for $\delta^{13}C$ (Fig. 2). SIA values of YT before and after this transition

Table 1. Predator and prey species sampled for white muscle tissue and analyzed for $\delta^{15}N$, $\delta^{13}C$, and mercury concentration [Hg]. $\delta^{13}C$ values were arithmetically-corrected ($\delta^{13}C'$) for effects of tissue lipid content, in accordance with Logan et al. (2008)

Species	Common name	Mean $\delta^{13}C'$ (SD)	Mean $\delta^{15}N$ (SD)	C:N (SD)	[Hg] (μg g^{-1} dw) (SD)	n
Predators						
Seriola dorsalis	California yellowtail	−16.8 (0.7)	16.6 (0.9)	3.4 (0.3)	1.27 (0.89)	72
Atractoscion nobilis	White seabass	−15.5 (0.2)	17.3 (0.5)	3.8 (0.1)	1.80 (0.60)	14
Thunnus albacares	Yellowfin tuna	−17.6 (0.3)	15.4 (0.8)	3.3 (0.2)	0.87 (0.24)	109
Prey (inshore)						
Sardinops sagax	Sardine	−16.9 (0.4)	13.9 (0.5)	3.3 (0.1)	0.10 (0.04)	13
Trachurus symmetricus	Jack mackerel	−18.2 (0.8)	14.2 (0.9)	3.9 (0.2)	0.09 (0.04)	5
Scomber japonicus	Pacific mackerel	−17.6 (0.9)	15.2 (1.2)	3.3 (0.1)	0.21 (0)	3
Doryteuthis opalescens	Market squid	−16.9 (0.7)	15.1 (0.9)	4.0 (0.3)	0.12 (0.03)	12
Atherinops affinis	Topsmelt	−16.5 (0.5)	15.5 (0.4)	3.7 (0)	0.25 (0.26)	3
Prey (offshore)						
Sardinops sagax	Sardine	−19.8 (0.2)	13.6 (0.6)	3.4 (0.2)	0.12 (0.06)	18
Trachurus symmetricus	Jack mackerel	−18.9 (0.6)	14.0 (0.8)	3.3 (0.1)	0.09 (0.05)	27
Scomber japonicus	Pacific mackerel	−18.3 (0.6)	14.4 (1.0)	3.1 (0.1)	0.08 (0.03)	16
Doryteuthis opalescens	Market squid	−18.6 (0.6)	14.5 (0.7)	3.6 (0.2)	0.18 (0.05)	21
Cololabis saira	Pacific saury	−18.9 (0.3)	13.2 (0.8)	3.3 (0.1)	0.07 (0.02)	20
Sebastes spp.	Rockfish juveniles	−19.1 (0.8)	13.8 (0.4)	3.3 (0.1)	0.14 (0.07)	7
Pleuroncodes planipes	Pelagic red crab	−18.6 (0.7)	11.6 (0.9)	4.6 (1.9)	0.13 (0.04)	13

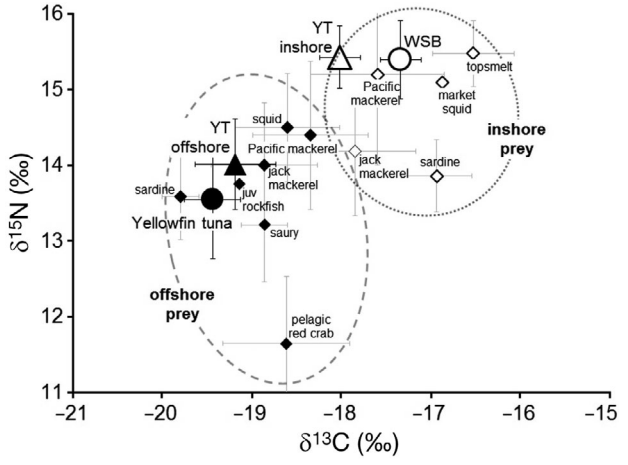

Fig. 1. $\delta^{13}C$ and $\delta^{15}N$ values (±SD) for coastal inshore and pelagic offshore predators and prey in the California Current Ecosystem. Large symbols depict predators: inshore and offshore California yellowtail *Seriola dorsalis* (YT), white seabass *Atractoscion nobilis* (WSB), and yellowfin tuna *Thunnus albacares* (YFT); smaller labelled symbols show inshore (open symbols) and offshore (filled symbols) prey, grouped by short- and long-dash ovals, respectively. Predator $\delta^{13}C$ and $\delta^{15}N$ values are diet-tissue discrimination factor (DTDF)-corrected (DTDF $\delta^{15}N$ = 1.9, $\delta^{13}C$ = 1.8) in accordance with Madigan et al. (2012)

range were significantly different (Mann-Whitney *U*-test, $p < 0.001$ for both $\delta^{13}C$ and $\delta^{15}N$).

Slopes of YT size versus SIA values were statistically different (linear regression); during the transition period R^2 values were highest for both $\delta^{15}N$ (R^2 = 0.53, p = 0.04) and $\delta^{13}C$ (R^2 = 0.33, p = 0.04), for $\delta^{15}N$ after the transition (R^2 = 0.12, p = 0.02), and for $\delta^{13}C$ after the transition (R^2 = 016, p = 0.03) (Fig. 2).

Discriminant analysis-based groupings of YT (based on $\delta^{13}C$ and $\delta^{15}N$) showed that most individuals reflected their catch region; 89% (24 of 27) and 73% (33 of 45) of inshore- and offshore-captured YT were grouped with inshore and offshore predators, respectively (Fig. 3). Offshore- and inshore-grouped YT showed overlap in YT sizes, predominately across the transitional size range (Fig. 3). Segmented regression showed that [Hg] change in YT was most abrupt at size 88.3 cm (Fig. 4). Mercury concentrations in YT categorized as inshore (1.81 ± 0.8m μg g^{-1} dw) were higher than in YT categorized as offshore (0.72 ± 0.53 μg g^{-1}) (Mann-Whitney *U*-test, $p < 0.0001$; Fig. 4), and inshore prey Hg concentrations (0.15 ± 0.07 μg g^{-1}) were generally higher than offshore prey (0.11 ± 0.04 μg g^{-1}), though this difference was not significant (Mann-Whitney *U*-test, p = 0.29) (Table 1). Length versus Hg relationships were significant for all groups represented in Fig. 4 (Spearman's rho, $p < 0.001$ for YT < 88.3 cm, YT > 88.3 cm, YFT, and WSB). Trends of Hg concentrations with size, in offshore and inshore YT, were similar to those of YFT and WSB, respectively (Fig. 4). However, slopes of YT size versus [Hg] were significantly

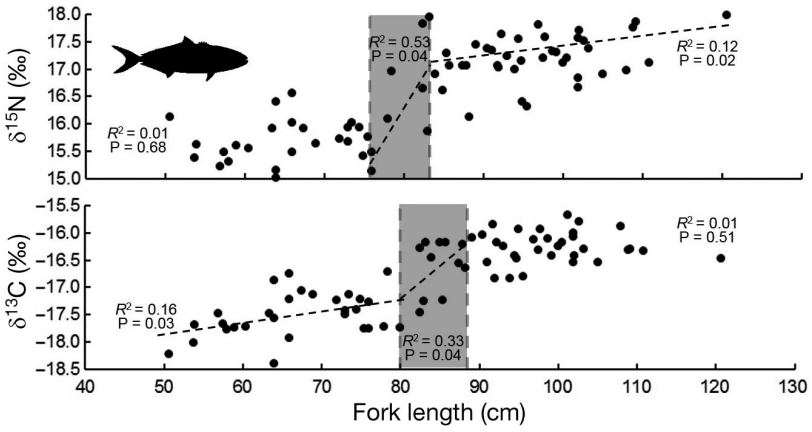

Fig. 2. Segmented regression for California yellowtail *Seriola dorsalis* (YT) size versus $\delta^{15}N$ and $\delta^{13}C$ of white muscle tissue. R^2 and p-value from linear regression are shown for each segment; dashed lines shown when trends were statistically significant ($p < 0.05$). Grey boxes show the 'transition phase' of YT from pelagic and highly migratory to more coastal and residential, based on results from segmented regression of $\delta^{15}N$ and $\delta^{13}C$ values

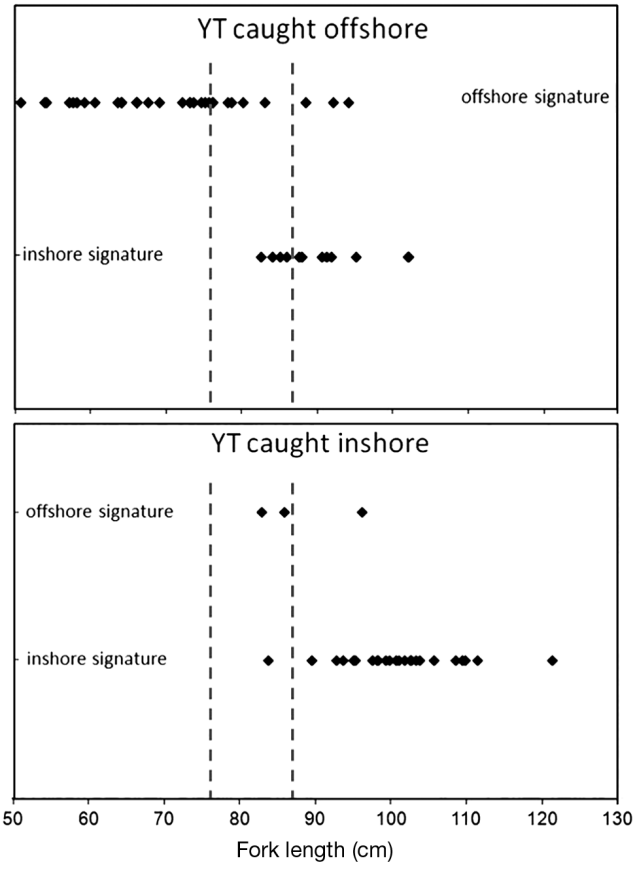

Fig. 3. California yellowtail *Seriola dorsalis* (YT) capture location (inshore or offshore) compared to discriminant analysis characterization as offshore or inshore. Groupings based on discriminant analysis using YT $\delta^{13}C$ and $\delta^{15}N$ values compared to $\delta^{13}C$ and $\delta^{15}N$ values of yellowfin tuna *Thunnus albacares* (offshore) and white seabass *Atractoscion nobilis* (inshore). Grey dashed lines: YT sizes at stable isotope analysis (SIA)-defined transition period from migrant to resident

different from YFT, with a higher slope for YT (ANCOVA, $F = 10.66$, $p = 0.001$), while slopes of size versus [Hg] were not statistically different between larger YT and WSB (ANCOVA, $F = 0.29$, $p = 0.59$)

Conventional tagging

Conventional tags were deployed on 26 inshore-caught YT (77 to 98 cm; 87.7 ± 5.5 cm) and 22 offshore-caught YT (45 to 59 cm; 53.3 ± 4.4 cm). All inshore YT were captured in association with anchored kelp beds in the SCB, in close proximity to the San Diego-Scripps Coastal Marine Protected Area. All offshore YT were captured in association with floating kelp mats. Angler-estimated time out of the water was ~2 min, and all tagged YT were observed to swim off in good condition. One YT immediately succumbed to predation from a California sea lion *Zalophus californianus*, but the YT body was immediately recovered and the tag removed.

A total of 15 tags were recaptured: 6 of 26 (23%) inshore-caught YT and 9 of 22 (41%) offshore-caught YT. Anglers reported recapture location and date verbally, and no muscle tissue from recaptured YT was available for SIA or Hg analysis. Time-at-liberty for all recaptured YT ranged from 1 to 556 d (188 ± 183 d) and net displacement ranged from 2.5 to 198.2 km (43.3 ± 54.4 km). Offshore-tagged YT were significantly smaller (44.9 to 59.2 cm; 54.8 ± 4.1 cm) than inshore-tagged YT (82.5 to 98.0 cm; 89.7 ± 6.9 cm) (Mann-Whitney *U*-test, $p < 0.001$) and offshore-tagged YT traveled significantly further (0.2 to 7.2 km d^{-1}; 1.6 ± 2.2 km d^{-1}) than inshore-tagged YT (<0.1 to 0.4 km d^{-1}; 0.1 ± 0.1 km d^{-1}) (Fig. 5a). All inshore-tagged YT were recaptured inshore, while 3 of 9 offshore-tagged YT were recaptured inshore (Fig. 5b).

DISCUSSION

The combination of SIA, conventional tagging, and Hg analyses provided insight into life history dynamics of YT. The observation of a habitat shift over a specific size range identifies the sizes and ages at which these shifts occur in present-day YT populations, indicating that YT can influence both pelagic and coastal ecosystems depending on life stage. These

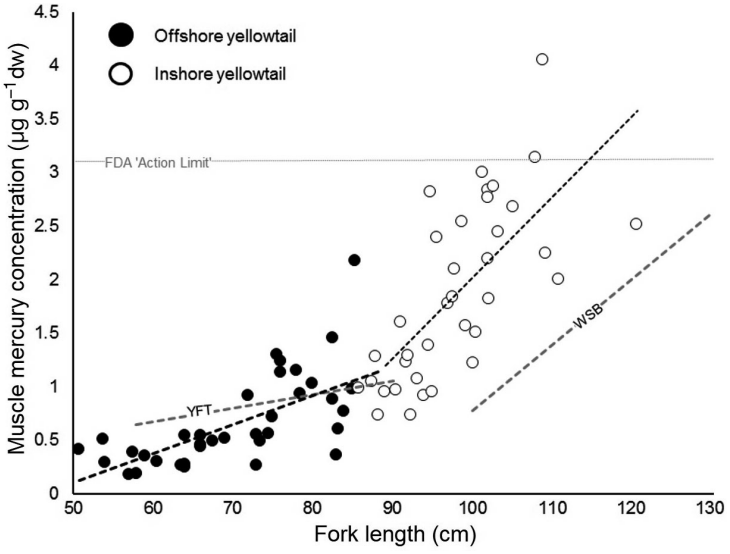

Fig. 4. Mercury concentrations [Hg] in muscle of California yellowtail *Seriola dorsalis* (YT). Inshore YT [Hg] was significantly higher (Mann-Whitney *U*-test, $p < 0.001$) than offshore YT [Hg] with several individuals approaching or exceeding the FDA 'action limit' of ~3.1 µg g^{-1} dry weight, dw (light gray line). Shown for comparison are linear fits to [Hg] measured here for inshore (white seabass *Atractoscion nobilis*; WSB) and offshore (yellowfin tuna *Thunnus albacares*; YFT) predators

basic life history parameters provide the basis for better assessment of movements and population size.

The higher $\delta^{15}N$ and $\delta^{13}C$ values of inshore versus offshore prey were analogous to CCE predators yellowfin tuna and white seabass. Discriminant analysis of $\delta^{15}N$ and $\delta^{13}C$ values combined with conventional tagging results support the interpretation of the isotopic shift in YT of sizes 76 to 87.5 cm as a result of a shift from offshore to inshore habitat. There was substantial variability of $\delta^{15}N$ and $\delta^{13}C$ values during the phase of transition from offshore to inshore foraging, which may be due to natural variability in the timing of habitat shifts and the turnover time (~1 to 1.5 yr for complete turnover) of $\delta^{15}N$ and $\delta^{13}C$ in muscle of large, active marine fish (Madigan et al. 2012).

The size ranges of YT sampled in inshore versus offshore habitat provided preliminary evidence of habitat segregation, with larger YT inshore (99 ± 9 cm) compared to offshore (80 ± 14 cm). The $\delta^{15}N$ and $\delta^{13}C$ values of YT caught inshore largely reflected the inshore isotopic signature, with 3 individuals having lower $\delta^{15}N$ and $\delta^{13}C$ suggesting more recent immigration from offshore waters. In offshore-caught YT, all small individuals (<80 cm) reflected their region of capture. However, a substantial number of larger (>80 cm) YT caught offshore reflected an inshore isotopic signature, suggesting that offshore presence of larger YT largely represents short forays into pelagic habitats.

Conventional tagging results are in agreement with the ontogenetic habitat shift inferred from SIA, with smaller fish (45 to 59 cm) tagged offshore and moving further than larger fish (83 to 98 cm) tagged inshore. Isotopic analyses show that larger adults associate with inshore habitats, which are often kelp beds in the study area. Since there are contiguous kelp beds along the southern California and Mexican

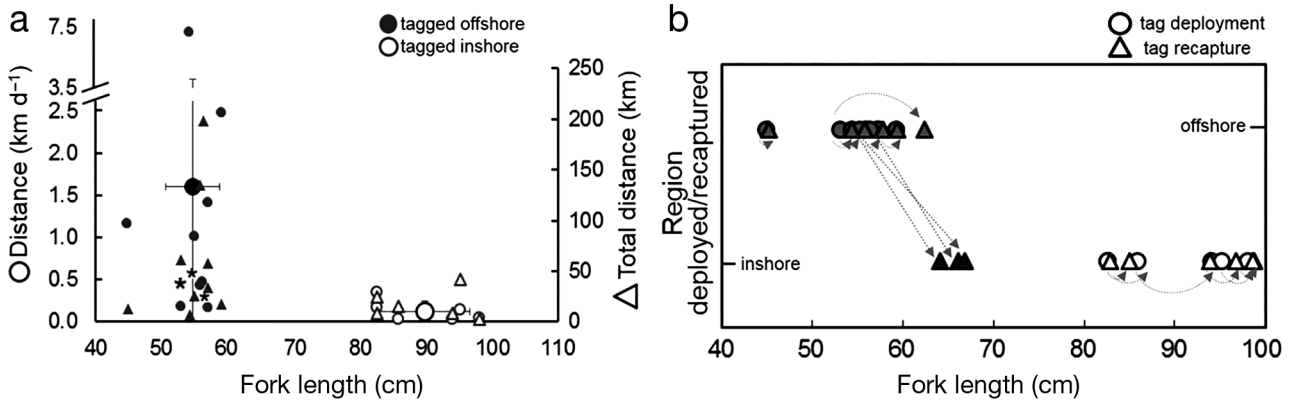

Fig. 5. Conventional tagging results for California yellowtail *Seriola dorsalis* (YT) in the California Current Ecosystem. (a) Overall displacement rates (circles) and total displacement (triangles) were higher for YT tagged in offshore (filled symbols) versus inshore (open symbols) habitats. Larger circles show mean size and displacement rate (mean ± SD) for offshore and inshore groups. Asterisks (*) show the 3 offshore-tagged fish that were recaptured inshore. (b) All inshore YT deployments (open circles) were recovered inshore (open triangles), while 3 offshore-tagged YT were recaptured in inshore habitat (see arrows; = asterisks in (a)). YT fork length at tag deployment was measured, while length at recapture was estimated by growth rates in Baxter (1960)

coastlines, these YT could still make long-distance migrations within and/or along inshore habitats. However, conventional tag results suggest that larger YT movements are limited to relatively constrained regions. Three offshore-tagged YT were recaptured inshore. These 3 fish were among the larger offshore-tagged recaptures (>65 cm), but their sizes at recapture were smaller than the offshore to inshore habitat shift inferred from SIA. Unfortunately, no tagged and recaptured YT fell in the habitat transition size range of 76 to 88 cm. Hg concentrations of prey were higher inshore than offshore, and Hg concentrations in YT muscle began to increase as individual fish reached 75 to 90 cm (maximum slope increase at 88.3 cm according to segmented regression), corresponding to ~4 to 6 yr of age (Baxter 1960). Increasing Hg concentrations are likely driven at least in part by age-based bioaccumulation, habitat, and prey differences (Karimi et al. 2012, Lavoie et al. 2013); Hg concentrations in younger YT were similar to global values reported for groundfish (e.g. lingcod, sablefish) while larger YT were more similar to grouper and some sharks (Karimi et al. 2012). Hg concentrations of YT classified as inshore and offshore were analogous to similarly sized inshore and offshore predators white seabass and yellowfin tuna, corroborating conclusions of an ontogenetic habitat shift from offshore to inshore waters in YT.

Isotopic and tag-based inferences of a highly migratory juvenile phase followed by more residential behavior in older YT supports results of a tagging study in the 1950s by Baxter (1960). In that study, YT were divided into 3 broad size categories: 30 to 60 cm, 61 to 90 cm, and >90 cm. The smallest YT (30 to 60 cm, largely unavailable in this study) showed minimal movement, while most in the second group (61 to 90 cm) were reported to have moved >50 miles (~80 km). In that study, no individual YT in the >91 cm group moved further than 80 km and all recoveries were reported as 'very close to the point of initial release' (Baxter 1960, p. 77). Our results generally agree with those historic data, and provide retrospective insights into the past movements of individual YT using $\delta^{15}N$ and $\delta^{13}C$ values in the context of local prey and predator values.

Combined with previous studies on larval abundance (Sumida et al. 1985) and adult movement (Baxter 1960), results presented here provide a fuller picture of YT life history. Based on observations of larvae, YT appear to spawn largely in waters off Mexico, though spawning off southern California was inferred in some years (Baxter 1960, Sumida et al. 1985), and large, mature YT with enlarged gonads are found in the SCB (O. Snodgrass pers. obs.). There is limited information on habitat use for YT <30 cm, but growth rates suggest that YT may reach this size by 4 to 6 mo (Baxter 1960). YT of sizes ≥50 cm (>1 yr old) are upper trophic-level predators of fish, cephalopods, and crustaceans in the CCE (Baxter 1960). Some YT are sexually mature at 50 cm, and all by 63 cm (Baxter 1960), indicating that YT in the migratory life stage are a mix of juveniles and adults. YT settling in coastal habitats (76 to 88 cm) are therefore all spawning size. Thus adult YT may spawn inshore locally or make occasional migrations to suitable offshore spawning habitat.

Shifting from pelagic offshore migrants to coastal inshore residents will make regional YT ecosystem roles life-stage-dependent. Like most juvenile fish, larval and juvenile YT (age 0–1) likely serve as potential prey for larger predators. By age 1, YT reach ~50 cm and become upper trophic-level predators in pelagic habitats, as are similarly sized yellowfin, bluefin, and albacore tunas (*Thunnus* spp.) that feed on fishes, cephalopods, and crustaceans in the offshore CCE (Madigan et al. 2015b). Pelagic YT were mostly captured in association with drifting kelp mats, which may serve as fish aggregating devices (FADs) in the pelagic CCE environment. Kelp mats in the SCB may serve as both refuge for larval/juvenile YT and as forage resources for larger YT, as kelp mats support metapopulations of both coastal and pelagic fish larvae and juveniles (e.g. *Sebastes* spp., jack mackerel, halfmoon *Medialuna californiensis*) (Hobday 2000). Kelp mat associated YT may prey substantially on associated fish assemblages, potentially affecting fish dispersal and recruitment.

In contrast to their roles as pelagic juveniles, larger YT will likely shape local kelp forest ecosystem structure as one of the predominant apex predators in their environment. In coastal California kelp forest food webs, YT share apex predator roles with marine mammals (harbor seals and sea lions), seabirds, and large sharks and teleosts (Graham 2004). Previous diet studies show jack mackerel, Pacific mackerel, sardine, and anchovy as the primary components of YT diet (Baxter 1960), all of which can be seasonally available in kelp forest ecosystems. YT also feed on common kelp forest inhabitants (e.g. small rockfish, lizardfish *Synodus lucio-cepsis*, butterfish *Peprilus simillimus*, blacksmith *Chromis punctipinnis*, señorita *Oxyjulis californica*), illustrating the potential for YT to exert top-down predation effects in kelp forest ecosystems. The significant increase in YT $\delta^{15}N$ after the transition to

residential habitats also presents the possibility that YT trophic level increases with size within these coastal ecosystems. The abundance of residential YT (4 to 13 yr old based on size; Baxter 1960) will thus influence this species' function as a top predator in its 'home' region for much of its lifespan. Effects of YT on kelp forest food webs have not been examined, but negative impacts of predator removal have been demonstrated in California kelp forests and other temperate kelp ecosystems (Steneck et al. 2002). Potential food web effects also may have been higher in the past, when some large predators were more abundant (Dayton et al. 1998), and future food web effects in kelp forests will be impacted by climate conditions (Byrnes et al. 2011).

The benefits of a shift from migratory pelagic to residential coastal behavior are difficult to measure and quantitatively assess. However, conjectures can be made based on physiology, ecology, and previous migration studies. Small YT likely migrate following ideal physiological sea surface temperatures, then settle into regional habitats as larger fish that can generally tolerate wider temperature ranges (Angilletta & Dunham 2003). Migration of young YT may act as an active dispersal mechanism to broaden distribution and locate ideal inshore habitat for residency. Historically, this may have allowed avoidance of predation in kelp beds by large teleosts (e.g. broomtail grouper *Mycteroperca xenarcha*, black sea bass *Stereolepis gigas*), elasmobranchs (e.g. sevengill shark *Notorynchus cepedianus*, tope shark *Galeorhinus galeus*), and marine mammals (e.g. sea lions). Predator avoidance has been shown to be a driver of ontogenetic habitat shifts in freshwater fish (Byström et al. 2003), sharks (Andrews et al. 2010, Grubbs 2010), and reef-associated marine teleosts (Dahlgren & Eggleston 2000). In pelagic habitats, sharks would likely be primary predators of YT, though there is minimal evidence of predation on YT by offshore sharks in the present-day CCE (Preti et al. 2012). Therefore, pelagic habitats may provide a more beneficial tradeoff between predator avoidance and prey availability, with fewer large predators than coastal kelp forest communities, less competition with larger conspecifics, and adequate prey resources, especially when associated with floating kelp mats. When larger YT are caught offshore, it is usually in summer and coincides with warming waters and the arrival of other pelagic predators migrating into the productive CCE to forage (Block et al. 2011).

Larger residential YT are caught in coastal waters year-round, including the coldest winter months (O. Snodgrass pers. obs.). Larger YT may benefit from the diversity and abundance of prey in kelp forest communities that provide a year-round food source. Abundant schooling fishes (e.g. mackerel, sardine, and topsmelt), kelp forest associated species, and squid spawning migrations to inshore waters likely provide year-round forage for coastal YT. A previous study (Baxter 1960) and author observations confirm diverse feeding in coastal YT, including rockfish, halfmoon, jacksmelt, blacksmith, isopods, and cusk eels. Residential association with physical structure at larger sizes is somewhat similar to yellowfin tuna in the CCE, which show a migratory period followed by a relatively residential period at specific islands, banks, and seamounts (Schaefer et al. 2011). Movements here can be compared to congeners in New Zealand (*Seriola lalandi*; colloquially 'yellowtail kingfish') which have been conventionally tagged in extensive cooperative efforts (Gillanders et al. 2001, Holdsworth et al. 2016). Gillanders et al. (2001) reported the most movement in fish 75 to 85 cm, while Holdsworth et al. (2016) showed greatest movement in smaller fish and residential behavior in larger fish with the inclusion of larger (>100 cm) YT. Thus, the observed shift in habitat seems to be conserved in YT species across ocean basins.

Offshore, migratory YT and pelagic yellowfin tuna had similar Hg trends at overlapping sizes. At 88.3 cm, YT mercury concentrations increased sharply, suggesting that increasing mercury in YT >88 cm may at least partially be due to higher Hg prey inshore. Over the size range of larger fish measured (100 to 140 cm), a similar increase in Hg was detected in white seabass, which is consistent with observations of decreasing Hg concentrations with increased distance from coastlines in multiple ocean basins, including the North Pacific (Hammerschmidt & Fitzgerald 2006, Sunderland & Mason 2007). Since some larger YT exceed the FDA 'action limit' (defined as the concentration above which the FDA will take action to remove products from markets), the higher concentration in large YT can be taken into account for seafood consumers concerned with mercury intake.

Previous assessments of YT catch have suggested a much higher recreational catch than commercial, and described the California catch as entirely dependent on migrants from Mexican waters (Collins 1973). While the existence of philopatry in YT is unknown, the pelagic phase at least presents the potential to replenish distant, overfished areas. This may partially explain the ongoing health of the YT population in the CCE, and past tagging has shown a

large influx of YT from southern regions, the Cedros Island area, in spring, fall, and summer (see Figs. 33, 34, 36, & 38 in Baxter 1960). However, residential behavior in large fish also presents the possibility of contributions from southern California YT to spawning stock biomass. Previous larval density assessments showed highest concentration off Punta Eugenia, Baja CA (~25° N), but larvae were observed off southern California as far north as Point Conception (~34.5° N) (Sumida et al. 1985). Advances in genetic markers (e.g. microsatellites) may provide further evidence for localized residential YT populations; recent studies show some mixing between Gulf of California YT and Pacific Baja YT, a higher degree of mixing between California and Baja-caught YT, and minimal mixing between California-caught and Gulf of California YT (Purcell et al. 2015).

To date, very little effort has been applied to understanding the complex ecology of one of California's iconic recreational gamefish. Our study demonstrates the efficacy of both chemical tracers and conventional tagging techniques in future studies of YT and/or similar species. The relative ease of handling and high tag return rates (23% inshore, 41% offshore) suggest that electronic tagging studies of this species could be successful. Residential behavior of large fish suggest that size distributions of YT populations may vary on regional and seasonal scales. Tagging with acoustic telemetry tags, in conjunction with an acoustic receiver network, could be used to evaluate the degree and potential benefits of YT association with recently established marine protected areas. Electronic tagging, higher resolution chemical tracer approaches, and extensive sampling efforts over broader geographical scales could provide further insight into finer-scale movement dynamics of this ecologically and economically valuable predator species.

Acknowledgements. NOAA staff and volunteers assisted with sample collections, and S. Zegers assisted with sample preparation. N. Wallsgrove and W. Ko assisted with isotope analysis. S. Kohin and J. Wraith provided floy tags and recapture support, and recreational anglers P. Holmes, D. Fuller, J. Bell, M. Medak, N. Ben-Aderet, L. Belquist, K. Nakada, B. Brightenburg, and A. Ljubovic assisted with tag deployments. Conventional tagging results were made possible by the recreational anglers in southern California that caught tagged fish and reported the recapture location and date. R. Olson provided encouragement and advice. Funding was provided by the John & Elaine French HUCE Fellowship to D.J.M. and by NSF OCE1634024 to N.S.F. All research and associated tissue sampling was carried out under the State of California Department of Fish and Wildlife permit #SC-12372 issued to the NOAA SWFSC.

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Editorial responsibility: Keith Hobson, London, Ontario, Canada

Submitted: August 14, 2017; Accepted: April 7, 2018
Proofs received from author(s): June 4, 2018