

## Depth distribution and temperature preferences of wahoo (*Acanthocybium solandri*) off Baja California Sur, Mexico

Chugey A. Sepulveda · Scott A. Aalbers ·  
Sofia Ortega-Garcia · Nicholas C. Wegner ·  
Diego Bernal

Received: 29 April 2010 / Accepted: 23 December 2010 / Published online: 18 January 2011  
© Springer-Verlag 2011

**Abstract** The depth distribution and temperature preferences of wahoo (*Acanthocybium solandri*) were quantified in the eastern North Pacific using archival tags. One hundred and eight data-loggers were deployed on wahoo (105–165-cm fork length) from 2005 to 2008 at three locations off of the coast of Baja California Sur, Mexico (Alijos Rocks, 25°00'N/115°45'W; Magdalena Bay Ridge, 25°55'N/113°21'W; Hurricane Bank, 16°51'N/117°29'W). Twenty-five tagged individuals (23%) were recaptured within close proximity (<20 km) of their release sites. Collectively, depth and temperature data from 499 days revealed a predominant distribution within the upper mixed layer, with an average ( $\pm$ SD) depth of  $18 \pm 4$  m during the day and  $17 \pm 6$  m at night. Wahoo spent 99.2% of the daytime and 97.9% of night above the thermocline, and the greatest depth achieved by any fish was 253 m. Mean dive duration ( $3.8 \pm 2.9$  vs.  $2.3 \pm 0.8$  min) and the vertical rate of movement ( $3.8 \pm 1.3$  vs.  $3.0 \pm 0.5$  m min<sup>-1</sup>) were greater at night when compared to day. Ambient

temperatures obtained from tag records ranged from 11.1 to 27.9°C, with an average of  $25.0 \pm 1.1$ °C. These data identify the importance of the warm, upper mixed layer for the wahoo. High recapture rates proximal to the deployment sites suggest seasonal site fidelity and reveal the economic importance of this resource to both commercial and recreational fisheries of the region.

### Introduction

The wahoo *Acanthocybium solandri* is a pelagic, highly migratory species of the family Scombridae broadly distributed throughout tropical and subtropical oceans (Hogarth 1976; Collette and Nauen 1983; Garber et al. 2005; McBride et al. 2008). Recent work on population connectivity and genetic structure propose that the wahoo represents a single circumglobal population (Theisen et al. 2008). Studies on life history suggest wahoo to be a fast-growing and relatively short-lived pelagic predator that experiences high rates of natural and fishing mortality (Hogarth 1976; Nash et al. 2002; Oxenford et al. 2003). Like many other oceanic predators (i.e., tunas, billfishes), the wahoo has a number of morphological and physiological adaptations related to fast burst swimming (Walters and Fierstine 1964; Magnuson 1978; Wegner et al. 2006; Wegner et al. 2010), which consequently makes it a prized target among recreational fishers. Due to its large size and high food value, the wahoo is also landed in many commercial operations (Takenaka et al. 1984; Luckhurst and Trott 2000; McBride et al. 2008; Uchiyama and Boggs 2006).

Throughout their extensive range, wahoo support directed recreational and artisanal fisheries and are a valuable incidental catch in both purse seine and longline fisheries

Communicated by S. Garthe.

C. A. Sepulveda (✉) · S. A. Aalbers  
Pfleger Institute of Environmental Research,  
315 N. Clementine, Oceanside, CA 92054, USA  
e-mail: Chugey@pier.org

S. Ortega-Garcia  
Centro Interdisciplinario de Ciencias Marinas-IPN. Av. IPN s/n  
Col. Playa Palo de Santa Rita, 23096 La Paz, BCS, México

N. C. Wegner  
Scripps Institution of Oceanography,  
La Jolla, CA 92093, USA

D. Bernal  
University of Massachusetts, Dartmouth,  
North Dartmouth, MA 02747-2300, USA

(Oxenford et al. 2003; Viana et al. 2008). Although wahoo are not typically the primary target of large-scale commercial fishing operations, world aggregate landings have risen steadily over the past three decades (Oxenford et al. 2003; Uchiyama and Boggs 2006). In part, this is due to the wahoo's role as a common bycatch species in tuna purse seine fisheries [in particular, operations associated with sets on natural and man-made fish aggregating devices (FADs)] (Maunder and Harley 2006). The increased use and reliance upon FADs in commercial fisheries has recently highlighted the importance floating objects play in the ecology of open ocean predators like the wahoo (Marsac et al. 2000; Menard et al. 2000; Dagorn et al. 2007).

Along the coast of Baja California Sur, the wahoo plays an important role in recreational fisheries supporting private and charter vessels as well as commercial passenger fishing vessels (CPFVs) operating out of San Diego, California (also known as the San Diego long-range fleet). Recent concern has been expressed over the lack of biological and stock information available for the wahoo in the Pacific with several questions related to its migratory and regional population status remaining unanswered (Garber et al. 2005; WPRFMC 2009).

Despite recent work that highlights the highly dispersive capabilities of wahoo at all life stages (Theisen et al. 2008), little is known regarding wahoo movements (vertical or horizontal) in the Pacific. To date, the limited tagging data available from wahoo in the Pacific suggests that they are highly migratory, with movements of over 2,500 km reported (NMFS 1999). Despite evidence of association with floating objects and subsurface features [i.e., seamounts, banks, islands; (Iversen and Yoshida 1957; Oxenford et al. 2003)], it is not known whether wahoo exhibit site fidelity when proximal to offshore seamounts (i.e., bathymetric features) and whether these areas support resident populations. Further, information on wahoo fine- and course-scale movements is necessary for understanding questions related to localized depletion and regional abundance in the eastern North Pacific (ENP). Such information is required to adequately assess fisheries impacts and can provide valuable insight into the ecology, life history, and movement patterns of this species in the ENP. Therefore, the objectives of this

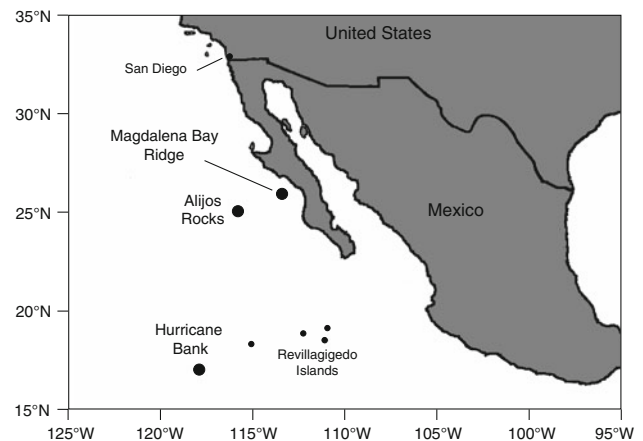
collaborative study were to use archival tags to assess depth distribution and associated temperature preferences of wahoo near particular oceanic features of the ENP.

## Methods

### Deployments

A total of 108 archival tags were deployed at three locations in the eastern North Pacific from October 2005 to October 2008 (Table 1, Fig. 1). All tags were deployed on wahoo captured by hook and line around offshore seamounts and pinnacles. Tagging locations were chosen based on wahoo availability and a heightened presence of commercial and recreational fishing operations. For all deployments, only wahoo hooked in the mouth and in good physical condition (e.g., no hook damage) were selected for the tagging experiments.

Forty-two archival tags were deployed at Alijos Rocks (25°00'N/115°45'W) during October of 2005. Alijos Rocks is an offshore pinnacle located 350 km west of Cabo San Lazaro, Baja California Sur. This location is a common destination for the San Diego long-range fleet (SDLRF) as



**Fig. 1** Map showing wahoo tag deployment sites (*large dots*) in the eastern North Pacific: Alijos Rocks, Magdalena Bay Ridge, Hurricane Bank. Other points of interest (*small dots*) San Diego, Revillagigedo Islands

**Table 1** Wahoo tag deployment information

Tagging trip	Deployment location	Number of tags deployed	Tag placement	Tag type	Tag sampling frequency ( $\text{min}^{-1}$ )
October 2005	Alijos Rocks	42	Intraperitoneal	Star-Oddi milli-TD	2
October 2005	Magdalena Bay Ridge	8	Intraperitoneal	Star-Oddi milli-TD	2
October 2006	Magdalena Bay Ridge	19	External	Cefas G-5 DST	1
January 2008	Hurricane Bank	18	External	Cefas G-5 DST	1
November 2009	Hurricane Bank	21	External	Cefas G-5 long-life DST	1

well as Mexican purse seine vessels targeting tuna. All tags deployed at Alijos Rocks were internally implanted within the peritoneal cavity using techniques described by Schaefer and Fuller (2002).

Twenty-seven archival tags were deployed in October of 2005 and 2006 along the Magdalena Bay Ridge ( $\sim 25^{\circ}55'N/113^{\circ}21'W$ ) Baja California Sur, Mexico. 'The Ridge' is an extensive subsurface bank that runs from approximately 100 km west of Punta Santo Domingo adjacent to the Baja coast toward Bahia Magdalena. A total of 39 archival tags were deployed on two trips to the Hurricane Bank ( $16^{\circ}51'N/117^{\circ}29'W$ ) in January and November, 2008. The Hurricane Bank is an offshore seamount located  $\sim 1,000$  km southwest of Cabo San Lucas, Baja California Sur, Mexico. The Ridge and Hurricane Bank are localities commonly fished by the SDLRF, as well as commercial longline and purse seine vessels. After the low return rates observed from the 2005 tag deployments (2%), all subsequent archival deployments were externally affixed in the dorsal musculature to reduce handling time and stress to the fish.

#### Tag types, attachment methods, and sampling regime

Tagged wahoo were outfitted with both an archival data storage tag (DST) and a conventional identification marker (FIM-96; Floy Tag Inc. Seattle, WA, USA). Three types of DSTs were used in this study: Star-Oddi DST milli-TD (Star-Oddi, Reykjavik, Iceland); Cefas G-5 (Cefas Technology Limited, Suffolk, UK), and Cefas G-5 extended-life DSTs. Star-Oddi tags were programmed to record depth and temperature measurements every 2 min, and the Cefas DSTs were programmed to sample depth and temperature once every minute.

Star-Oddi DSTs were surgically implanted into the peritoneal cavity of wahoo captured using recreational tackle at Alijos Rocks and the Magdalena Bay Ridge in October, 2005. After a brief ( $<10$  min) fight, fish were brought alongside the vessel and gently lifted onboard using a large nylon sling. Each specimen was placed in a V-board cradle and secured ventral side up allowing the gills to be irrigated with fresh seawater from a deck hose. Intraperitoneal tag placement followed the methods described previously for tunas (Schaefer and Fuller 2002). Incisions were closed using surgical grade sutures [Ethicon (PDS II), cutting cp-1] and 35W stainless steel skin staples (3M PGX-35W, St. Paul, MN, USA). Fork length (FL) was measured to the nearest cm, and the hook was removed prior to release. Total handling time onboard the vessel ranged from 65 to 135 s.

Cefas G-5 and Cefas G-5 long-life DSTs were externally affixed to wahoo in the dorsal musculature using an extended tagging pole, while the fish were lea

side of the vessel. Tag tethers consisted of stainless steel crimps, an 8-cm section of 100-kg plastic-coated stainless steel cable, and a black plastic umbrella anchor (Sepulveda et al. 2010).

#### Data analysis

Archived depth and temperature data were downloaded from tags, and summary statistics were calculated for each recaptured individual prior to conducting comparisons between tagging sites and deployment periods. Because of the small sample size ( $n = 1$ ) of the Alijos Rocks wahoo, and the internal tag implantation method, the 23 days of data collected were excluded from the collective temperature analyses. All records were assigned 'day' or 'night' values based on the time of civil twilight from the United States Naval Observatory database. Crepuscular periods were not analyzed separately as diurnal transitions in depth distribution were not evident during this period. Vertical rate of movement (VROM) was calculated for each fish as the mean difference of all subsequent 1-min depth records. Thermocline depth was estimated for each deployment site by calculating the difference between subsequent mean temperature values for each 1 m bin to determine the depth with the greatest  $\Delta T$  value. Thermocline values were subsequently verified through graphical inspection of the vertical temperature profiles and found to be consistent with published values for the region (Fielder 1992).

The number and duration of all dives as well as the percent of track record spent below the thermocline were assessed for all individuals using Access (Microsoft Office 2003, Seattle, Washington, USA). A dive was defined as any vertical excursion that exceeded the depth of the thermocline and remained at or below this depth for  $>2$  min. Contour plots of the joint distribution of depth and time were constructed to illustrate the general vertical trends for each tagging location over a 24-h period (MATLAB, R12). All values are indicated as mean  $\pm$  SD, and  $\alpha < 0.05$  was used to infer significance.

#### Results

A total of 108 electronic data-loggers were deployed in wahoo, ranging in size from 105 to 165 cm FL and 6–35 kg, at the three study sites between October, 2005 and November, 2008 (Table 1, Fig. 1). Twenty-five tagged individuals were recaptured by recreational and commercial fishers, resulting in an overall recapture rate of 23% (Table 2). Among the recaptured individuals, one tag failed to operate properly (wahoo #7) and two of the externally affixed archival tags were shed while at liberty (wahoo #14 and 19 only had conventional tags returned from fishers).

**Table 2** Wahoo recapture information and depth statistics

Fish	Date	Length (cm) (FL <sup>a</sup> )	Deployment location	Days at liberty	Recaptured by <sup>b</sup>	Max depth (m)	Mean depth (m)	±SD
1-478	10/3/2005	145	Alijos	23	SDLRF	106	8.9	7.9
2-715	10/10/2006	137	Ridge	4	PY	113	23	14.1
3-746	10/12/2006	127	Ridge	12	CPS	116	18	10.3
4-720	10/14/2006	126	Ridge	10	SDLRF	103	18.2	12.4
5-747	10/14/2006	137	Ridge	12	CPS	89	22	12.5
6-700	1/18/2008	155	Hurricane	15	CPS	132	17.3	16.4
7-000	1/18/2008	110	Hurricane	15	SDLRF	N/A <sup>c</sup>	N/A <sup>c</sup>	N/A <sup>c</sup>
8-728	1/18/2008	110	Hurricane	15	CPS	87	13.8	11.3
9-729	1/18/2008	112	Hurricane	21	CPS	126	16.5	15.0
10-741	1/18/2008	110	Hurricane	43	CPS	120	14.3	11.3
11-732	1/18/2008	142	Hurricane	11	SDLRF	97	14.1	10.7
12-733	1/18/2008	130	Hurricane	15	CPS	253	16.6	11.1
13-077	11/20/2008	120	Hurricane	27	SDLRF	106	16.7	9.9
14-000	11/20/2008	130	Hurricane	23	SDLRF	N/A <sup>c</sup>	N/A <sup>c</sup>	N/A <sup>c</sup>
15-089	11/20/2008	140	Hurricane	26	SDLRF	216	24.7	18.1
16-097	11/20/2008	135	Hurricane	21	SDLRF	184	21.6	17.9
17-100	11/20/2008	113	Hurricane	15	SDLRF	135	15.7	11.5
18-104	11/20/2008	135	Hurricane	14	SDLRF	127	23.8	18.4
19-000	11/20/2008	130	Hurricane	15	SDLRF	N/A <sup>c</sup>	N/A <sup>c</sup>	N/A <sup>c</sup>
20-116	11/20/2008	135	Hurricane	26	SDLRF	92	15.5	10.4
21-151	11/20/2008	116	Hurricane	29	SDLRF	131	17.8	14.5
22-202	11/20/2008	120	Hurricane	62	SDLRF	112	14.8	9.7
23-600	11/20/2008	130	Hurricane	68	SDLRF	103	18.6	13.1
24-604	11/20/2008	105	Hurricane	14	SDLRF	121	18.4	12.7
25-606	11/20/2008	135	Hurricane	16	SDLRF	113	14.1	11.7
							Mean ± SD	17.5 ± 3.8 m

<sup>a</sup> Length estimated from weight using Uchiyama and Boggs (2006)

<sup>b</sup> *SDLRF* San Diego long-range fleet, *PY* private yacht, *CPS* commercial purse seine vessel

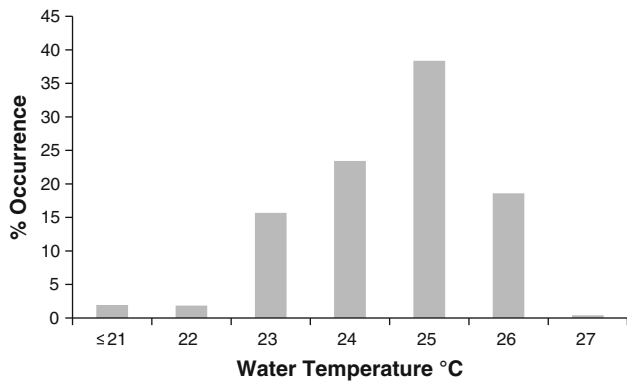
<sup>c</sup> Archived data was not obtained from this individual

Collectively, 499 days of archived depth and temperature data (1,338,136 observations) were compiled from all deployments. Of the recaptured individuals, 72% ( $n = 18$ ) were caught by recreational fishers and 28% ( $n = 7$ ) by Mexican flagged tuna purse seine vessels. Site- and season-specific recapture rates varied from a low of 2% (1 of 42) at Alijos Rocks to a high of 62% (13 of 21) in the fall of 2008 at the Hurricane Bank. All recaptures occurred proximal to the release sites (<20 km) following periods at liberty of up to 68 days (Table 2).

#### Cumulative vertical movement and temperature analyses

The cumulative mean depth (±SD) for all wahoo in this study was  $18 \pm 4$  m during the day and  $17 \pm 6$  m at night. Collectively, wahoo spent 99.2% of the daylight

hours and 97.9% of the night within the upper mixed layer, with only brief excursions recorded below the thermocline. Diel comparisons of diving activity for all sites with multiple datasets showed the mean dive duration was significantly greater at night ( $3.8 \pm 2.9$  min) when compared to day ( $2.3 \pm 0.8$  min) (Paired  $t$  test,  $p < 0.05$ ), while the average number of dive events (day and night) did not differ significantly among the sites. VROM was also greater at night ( $3.8 \pm 1.3$  m min<sup>-1</sup>) when compared to day ( $3.0 \pm 0.5$  m min<sup>-1</sup>) (Paired  $t$  test,  $p < 0.05$ ). Similarly, the maximum recorded dive duration at night (53 min) was also greater than that observed during the day (33 min). Collectively, tagged wahoo experienced water temperatures ranging from 11.1 to 27.9°C, with a mean of  $25.0 \pm 1.1$ °C. As a group, wahoo spent 98% of the track records within water temperatures  $\geq 22.0$ °C (Fig. 2).

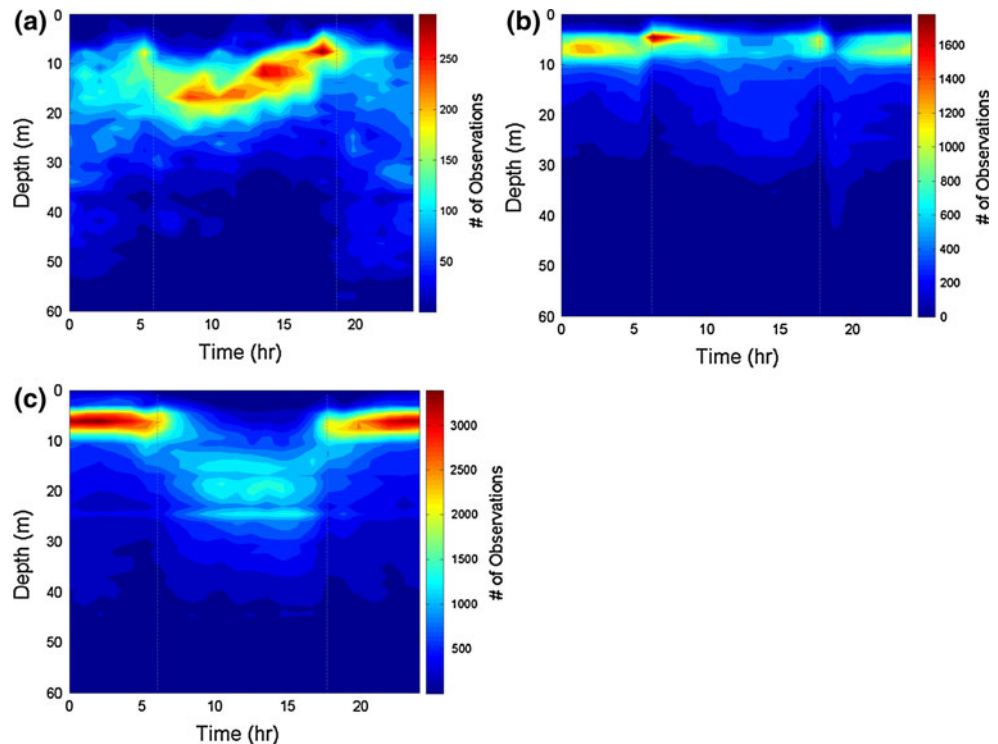


**Fig. 2** A histogram of the % occurrence at a specific water temperature for all wahoo with externally affixed archival tags

### Alijos Rocks

A single wahoo was recaptured at Alijos Rocks by a San Diego-based CPFV after 23 days at liberty yielding a 2% recovery rate for this site (Table 2). The mean depth ( $\pm$ SD) for the entire deployment was  $9 \pm 8$  m, and the maximum depth attained was 106 m. The diel depth distribution revealed similar average day ( $10 \text{ m} \pm 8$ ) and night ( $8 \text{ m} \pm 7$ ) depths. For the entire track period, the mean VROM was  $1.8 \text{ m min}^{-1}$  with similar average VROM values for both day ( $1.83 \pm 2.3 \text{ m min}^{-1}$ ) and night ( $1.7 \pm 2.3 \text{ m min}^{-1}$ ). Intraperitoneal temperature records ranged from 20.4 to 23.3°C with an average of  $22.8 \pm 0.4^\circ\text{C}$ .

**Fig. 3** A plot of the joint distribution of time and depth plotted over a 24-h period for all wahoo tagged at the Baja Ridge (a 45,434 observations), the Hurricane Bank in winter (b 163,549 observations), and fall (c 444,352 observations) of 2008. The vertical dashed line approximates sunrise and sunset



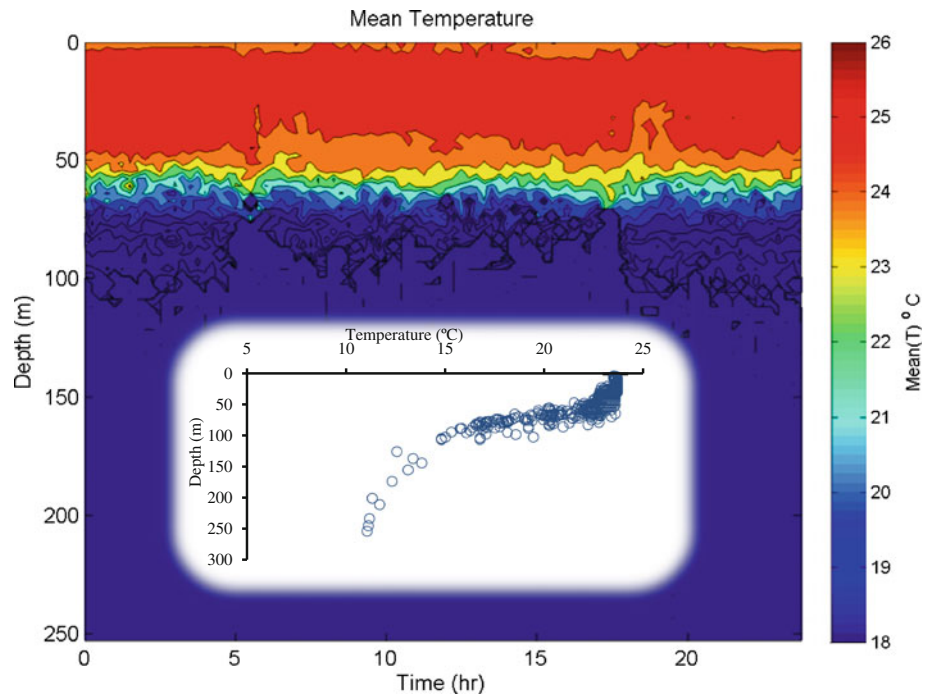
### Baja Ridge

Four wahoo were recaptured along the Baja Ridge resulting in 38 days of data and a 15% recapture rate for this site (Table 2, Fig. 3a). The cumulative mean depth was  $20 \pm 3$  m with a greater average night depth ( $24 \pm 4$  m) when compared to day ( $17 \pm 1$  m) (Paired *t* test,  $p < 0.05$ ). The Ridge wahoo spent more time below the thermocline at night ( $11.2 \pm 5.7\%$ ) than during the day ( $0.9 \pm 0.4\%$ ) (Paired *t* test,  $p < 0.05$ ). In addition, the mean VROM at night ( $5.5 \pm 1.2 \text{ m min}^{-1}$ ) was greater than day ( $3.0 \pm 0.5 \text{ m min}^{-1}$ ) (Paired *t* test,  $p < 0.05$ ). Other diel patterns include a greater average dive duration during the night ( $3.9 \pm 0.5$  min) compared to the day ( $2.0 \pm 0.3$  min) (Paired *t* test,  $p < 0.05$ ), with periods of up to 33 min spent below the thermocline (estimated thermocline depth was 44 m at this site). Archived temperature records ranged from 14.7 to 27.9°C with a mean of  $25.0 \pm 1.5^\circ\text{C}$ .

### Hurricane Bank

Two tagging cruises in January (winter) and November (fall) of 2008 resulted in a cumulative recapture rate of 52%, with 13 of the 21 tags (62%) recovered from the fall deployments (Tables 1, 2). Collectively, the Hurricane Bank deployments resulted in 438 days of depth and temperature data. For all Hurricane Bank deployments, the mean day and night depths were  $18 \pm 4$  and  $16 \pm 5$ , respectively. Figure 3b and c represent the joint

**Fig. 4** A plot of ambient temperature at depth for wahoo tagged at the Hurricane Bank and (*inset*) the vertical temperature gradient obtained from an archivally tagged wahoo (#12-733)



distribution of time and depth over a 24-h period for the wahoo deployments in winter and fall of 2008. Day and night depths were similar in winter, whereas the average day depth ( $20 \pm 3$  m) was greater than night ( $17 \pm 6$  m) for the fall deployments (Paired *t* test,  $p > 0.05$ ). The mean VROM for all Hurricane deployments was  $3.3 \pm 0.77$  m  $\text{min}^{-1}$  with wahoo exhibiting a greater VROM at night ( $3.5 \pm 0.9$  m  $\text{min}^{-1}$ ) than during the day ( $3.1 \pm 0.5$  m  $\text{min}^{-1}$ ) (Paired *t* test,  $p < 0.05$ ). Brief dives, averaging  $4.1 \pm 4.7$  min, were recorded to a maximum depth of 253 m at this location where water temperatures as low as  $11.1^\circ\text{C}$  were encountered. Ambient water temperature averaged  $25.0 \pm 0.9^\circ\text{C}$  and ranged from  $11.1$  to  $27.9^\circ\text{C}$ . Thermocline depth was estimated at 70 m in winter and 59 m in fall (Fig. 4).

## Discussion

The specific objectives of this study were to document the vertical distribution, movements and corresponding water temperature of wahoo tagged near bathymetric features (i.e., seamounts) in the ENP using archival tags. Despite differences in deployment time (seasons of the year) and location, the depth distribution was markedly similar among all individuals revealing a heightened presence in the upper mixed layer both during the day and night. Similarly, temperature records support a predominant warm-water existence ( $\geq 22^\circ\text{C}$ ), with only brief periods spent in cooler waters below the thermocline (Fig. 2). Although wahoo in the Atlantic (Theisen et al. 2008) and

Pacific (NMFS 1999) have been shown to undertake extensive horizontal movements, the individuals of this study did not emigrate from the tagging locations suggesting some degree of seasonal site fidelity for the seamounts in the ENP.

## Recapture rates

The collective recapture rate of 23% for this study is much higher than that reported for previous wahoo tagging studies (Oxenford et al. 2003) but is within the range of values reported for temperate and tropical tuna species of the ENP. Specifically, the recapture rate of this study was lower than that reported for bigeye tuna (*Thunnus obesus*; 30%, Schaefer and Fuller 2002) and yellowfin tuna (*Thunnus albacares*; 53%, Schaefer et al. 2007) and slightly higher than that of skipjack tuna (*Katsuwonus pelamis*; 18%, Schaefer and Fuller 2007). However, the site-specific recapture rates of this study varied considerably from 2% at Alijos Rocks to 62% for the fall deployments at the Hurricane Bank. The low tag recovery rate from Alijos Rocks was likely due to a combination of factors including the internal tag placement, high predator abundance as well as reduced fishing effort from the San Diego-based CPFVs in the fall of 2005 (personal communication; Captain Tom Rothery, San Diego, CA, USA). During the tagging operations at Alijos Rocks, large pelagic sharks were continuously observed near the tagging vessel, and several hooked wahoo were preyed upon during the fight. To minimize capture stress and reduce the duration of the tagging procedure (i.e., time on boat,

surgery), all deployments subsequent to the 2005 tagging cruise utilized an external attachment method similar to that employed by Horodysky and Graves (2005).

The high recapture rates observed at the Hurricane Bank in the winter (44%) and fall (62%) of 2008 were likely a product of several factors including heightened fishing effort, low rates of emigration, and the relatively small size of this isolated sea mount. During Hurricane Bank tagging operations, both SDLRF and commercial purse seine vessels were observed fishing around the seamount.

#### Depth distribution

Although depths of up to 253 m were recorded in this study, >98% of all depth records for both day and night periods were within the warm waters of the upper mixed layer. These data support previous reports which show wahoo catches predominantly from shallow-set hooks in longline operations (Nakano et al. 1997; Beverly et al. 2009). Similar vertical behaviors have been recorded for other pelagic, surface-oriented species like the sailfish (*Istiophorus platypterus*), whitetip shark (*Carcharhinus longimanus*), and mahi mahi (*Coryphaena hippurus*) (Schuck 1951; Hoolihan 2005; Bernal et al. 2009). Although differences in mean depth were identified among several of the study sites, the small degree to which the depth distributions varied with location, season, and time of day (<12 m) likely represents little ecological significance. Further, the high degree to which the vertical distributions overlapped at each location suggests that many of the observed depth trends may be in response to seasonal or environmental cues rather than site-specific or individual variability. As shown for other pelagic species, factors such as changes in oceanographic conditions, prey availability, and distribution all contribute to the vertical movements displayed by a species at different times and locations (Schaefer and Fuller 2002; Sepulveda et al. 2010).

The diel vertical distribution recorded in this work is similar to the surface-oriented behaviors described for both yellowfin tuna and skipjack tuna, two species that were present at all three deployment locations. Schaefer et al. (2007) identified a surface-oriented distribution behavior (referred to as “Type 1”) in 78% of the yellowfin tuna records from the ENP. Similarly, when associated with floating objects, skipjack tuna displayed a comparable movement pattern in which day and night distribution was typically above 100 m (Schaefer and Fuller 2007). However, unlike the yellowfin or skipjack tuna data, the wahoo of this study only demonstrated the surface-oriented distribution and did not reveal any periods of frequent diving below the thermocline. This may,

in part, be due to the wahoo's association with topographical features (i.e., banks, rides, high spots), as several tuna species have been shown to alter their vertical distribution when associated with both floating objects and topographical features (Schaefer and Fuller 2002; Musyl et al. 2003; Schaefer and Fuller 2007). Because all of the wahoo deployments and recaptures were made proximal to seamounts (i.e., banks), it may be that the movements recorded in this study are only indicative of wahoo that are associated with these features (i.e., high spots, ridges), further suggesting the need for additional deployments on fish that are not associated with topographical features. Similar findings have been shown for bigeye tuna when associated with banks off the Hawaiian archipelago (Musyl et al. 2003) as well as bigeye tuna associated with FADs in the ETP (Schaefer and Fuller 2002). Thus, it may be that open-school or un-associated wahoo may exhibit different depth distributions or diving characteristics than those presented in this study.

#### Temperature

The ambient temperatures recorded in this study fall within the values reported for the distribution and thermal range of this species (Collette and Nauen 1983; Bernal et al. 2009). The average maximum change in temperature ( $\Delta T$ ; SST-minimum temperature at depth) experienced as a result of diving ( $12.7 \pm 1.8^\circ\text{C}$ ) was similar to that commonly encountered by several tuna species (i.e., yellowfin tuna, skipjack tuna). However, the amount of time spent at depth was much less than that described for tunas (Holland et al. 1990, 1992; Dagorn et al. 2006; reviewed by Bernal et al. 2009). Because the wahoo does not have the capacity to elevate body temperature like the tunas and lamnid sharks (regional endothermy, Carey et al. 1971; Graham 1975), it may be that this species is physiologically less tolerable to prolonged exposure to colder temperatures and thus a factor contributing to the observed depth distribution of this study. However, several ectothermic species (i.e., blue shark *Prionace glauca*, bigeye thresher shark *Alopias superciliosus*, opah *Lampris guttatus*) have also been shown to tolerate extreme changes in ambient temperature for prolonged periods (Carey and Scharold 1990; Nakano et al. 2003; Polovina et al. 2007).

Due to the internal position (within the peritoneal cavity) of the archival tag in the individual wahoo recaptured at Alijos Rocks, the  $\Delta T$  associated with the dive records was not directly compared to the individuals with externally affixed tags. The resultant lag in  $\Delta T$  due to thermal inertia and the short duration of the relatively shallow dives (<100 m) prevented any accurate measures of ambient temperature at depth as well as the determination of the depth of the thermocline (Neill et al. 1976).

## Horizontal movements

All recaptures were reported within 20 km of the original deployment locations. The limited horizontal movements observed in this study suggest a relatively high level of seasonal site fidelity but may also be an artifact of the short duration of the deployments (4–68 days). The lack of emigration from the tagging sites may be attributed to several factors including high natural or tagging mortality rates, intense fishing effort at the deployment sites or possibly tag shedding, and issues with long-term tag retention. Oxenford et al. (2003) discussed the concept of seasonal feeding areas around seamounts in the Atlantic; it may be that a similar situation was observed in the present study. Another consideration is that tagged wahoo may have emigrated into areas of reduced fishing pressure and were never recaptured.

In the Pacific, a single conventionally tagged wahoo was shown to migrate 2,747 km in 198 days at liberty (NMFS 1999), illustrating the highly migratory potential of this species. Other tagging studies of shorter duration have also revealed significant horizontal movements off the Atlantic and Gulf of Mexico, with tagged wahoo moving from the northern Bahamas to the Carolinas within weeks (Theisen 2007). Nash et al. (2002) reported on a single wahoo at liberty for 10 months that moved only 64 km from the tagging location; however, it is not known whether this individual underwent any additional movements or if it remained proximal to the release site the entire time. In the Atlantic, it is suggested that wahoo seasonally migrate in response to changing SST's (Hogarth 1976; Oxenford et al. 2003). Similar seasonal movements are suspected in the ENP along Baja California, especially when wahoo are seasonally caught by CPFVs at higher latitudes during warm water years, as well as their absence at the same locations when conditions are not optimal (Pers. Comm. Captain T. Rothery, San Diego CA, USA). The lack of large-scale horizontal movements observed in this study may be a product of the consistent SST's recorded at each site and the paucity of data from periods of differing oceanic conditions (i.e., seasons, SSTs). Future long-term deployments over several seasons are needed to fully understand wahoo movement patterns along the coast of Baja California Sur.

## Feeding ecology and wahoo fisheries

Despite the lack of studies of wahoo gut contents in the ENP, the feeding ecology work to date suggests that wahoo prey upon a wide variety of pelagic fish species including small tunas (i.e., frigate tunas *Auxis* spp., yellowfin tuna and skipjack tuna) (Manooch and Hogarth 1983; Collette and Nauen 1983; Oxenford et al. 2003; Rudershausen et al.

2010). Observations made during the tagging cruises to the Hurricane Bank and along the Baja Ridge suggest that the wahoo movements were closely associated with schools of small tuna (skipjack tuna and frigate tuna) observed at the surface around the seamounts. For many of the wahoo deployments, a directed effort was made to fish proximal to the tuna aggregations, as wahoo catch increased near the tuna schools. Thus, it is not surprising that the wahoo depth distribution of this study closely resembles that described for skipjack tuna associated with floating objects in the ENP (Schaefer and Fuller 2007). Because horizontal and vertical movements are linked to prey abundance and distribution, it is also not surprising that several of the wahoo of this study were recaptured by tuna purse seine vessels operating near the seamounts. High seasonal site fidelity and the surface-oriented distribution recorded in this study further corroborate the wahoo's vulnerability to recreational and commercial fisheries of the ENP, especially those operations associated with recurrent activities at the same location. Further, it may be that purse seine operations around seamounts and possibly FADs have collectively contributed to the increased global landings of wahoo over the past few decades (Menard et al. 2000; Maunder and Harley 2006; Chassot et al. 2009).

## Management and future directions

This work provides insight into the movements and behaviors of a valuable resource of the ENP that has received little study to date. Although the wahoo may not be the primary focus of most large-scale commercial operations, the collective take from sport and commercial fisheries has increased over the past three decades fueling the need for information on the movement patterns and ecology of this species. In particular, knowledge of species-specific depth distributions, temperature preferences, vertical niche partitioning, and interspecific interactions are essential for a better understanding of the pelagic ecosystem. Moreover, behavioral, ecological, and oceanographic information of this nature are a prerequisite for increasing fishing gear specificity as well as understanding how potential gear modifications may alter catch composition. The movement data of this study strongly support the importance of the upper mixed layer to structure-associated wahoo in the ENP and raises important questions about whether these movement patterns are also present in wahoo that are not associated with bathymetric features. For this reason, we feel that future complimentary studies on non-associated wahoo, as well as individuals associated with natural or man-made floating objects, are necessary to fully comprehend the wahoo's ecological and environmental preferences in the ENP. Finally, the combination of high site-specific recapture rates and the evident seasonal site

fidelity reported in this study suggest that wahoo may be especially vulnerable to commercial and recreational operations that repeatedly target the same location during protracted time periods.

**Acknowledgments** We thank Tom Pflieger and Family, and the George T. Pflieger Foundation for their generous support for this project. Special thanks are offered to Captain Tommy Rothery and the crew of the F/V *Polaris Supreme* for their assistance during the tagging cruises. We also thank Captain Tommy Fullam, Victoria Wintrose, Lorraine Bohnet, Harry Okuda, and Dan Fuller for their help on various aspects of this work. We also thank Dr. Leonel Romero for his assistance with the graphic illustrations and Dr. J. Donley for her valuable comments on this manuscript. We thank COFAA-IPN for the support offered for one of the co-authors. All experiments were performed under the permits DGOPA13308.210905, DGOPA09974.260906, and DGOPA08071.310708 authorized by CONAPESCA.

## References

- Bernal D, Sepulveda C, Musyl M, Brill R (2009) The eco-physiology of swimming and movement patterns of tunas, billfishes, and large pelagic sharks. In: Domenici P, Kapurr D (eds) *Fish Locomotion—an etho-ecological perspective*. Science Publishers, Enfield, pp 436–483
- Beverly S, Curran D, Musyl M, Molonya B (2009) Effects of eliminating shallow hooks from tuna longline sets on target and non-target species in the Hawaii-based pelagic tuna fishery. *Fish Res* 96:281–288
- Carey FG, Scharold JV (1990) Movements of blue sharks, *Prionace glauca*, in depth and course. *Mar Biol* 106:329–342
- Carey FG, Teal JM, Kanwisher JW, Lawson KD (1971) Warm bodied fish. *Am Zool* 11:135–145
- Chassot E, Amandè MJ, Chavance P, Pianet R, Dédo RG (2009) Some preliminary results on tuna discards and bycatch in the French purse seine fishery of the eastern Atlantic Ocean. *Collect Vol Sci Pap ICCAT* 64(4):1054–1067
- Collette BB, Nauen CE (1983) *FAO species catalogue, vol 2. Scombrids of the world. An annotated and illustrated catalogue of tunas, mackerels, bonitos, and related species known to date.* FAO 125:1–137
- Dagorn L, Holland KN, Hallier JP, Taquet M, Moreno G, Sancho G, Itano DG, Aumeeruddy R, Girard C, Million J, Fonteneau A (2006) Deep diving behavior observed in yellowfin tuna (*Thunnus albacares*). *Aquat Living Resour* 19:85–88
- Dagorn L, Pincock D, Girard C, Holland K, Taque M, Sancho G, Itano D, Aumeeruddy R (2007) Satellite-linked acoustic receivers to observe behavior of fish in remote areas. *Aquat Living Resour* 20:307–312
- Fielder PC (1992) Seasonal climatologies and variability of eastern tropical Pacific surface waters. NOAA Tech Rep NMFS 109:1–65
- Garber AF, Tringali MD, Franks JS (2005) Population genetic and phylogeographic structure of wahoo, *Acanthocybium solandri*, from the western central Atlantic and central Pacific Oceans. *Mar Biol* 147:205–214
- Graham JG (1975) Heat exchange in the yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*, and the adaptive significance of elevated body temperatures. *Fish Bull* 72:219–229
- Hogarth WT (1976) Life history aspects of the wahoo, *Acanthocybium solandri* (Cuvier and Valenciennes), from the coast of North Carolina. Dissertation, North Carolina State University
- Holland KN, Brill RW, Chang RKC (1990) Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregation devices. *Fish Bull* 88:493–507
- Holland KN, Brill RW, Chang RKC, Sibert JR, Fournier D (1992) Physiological and behavioral thermoregulation in bigeye tuna, *Thunnus obesus*. *Nature* 358:410–412
- Hoolihan J (2005) Horizontal and vertical movements of sailfish (*Istiophorus platypterus*) in the Arabian Gulf, determined by ultrasonic and pop-up satellite tagging. *Mar Biol* 146:1015–1029
- Horodysky AZ, Graves JE (2005) Application of popup satellite archival tag technology to estimate postrelease survival of white marlin (*Tetrapturus albidus*) caught on circle and straight-shank (“J”) hooks in the western North Atlantic recreational fishery. *Fish Bull* 103:84–96
- Iversen ES, Yoshida HO (1957) Notes on the biology of wahoo in the Line Islands. *Pac Sci* X1:370–379
- Luckhurst BE, Trott T (2000) Bermuda’s commercial line fishery for wahoo and dolphinfish: landings, seasonality and catch per unit effort trends. *Proc Gulf Caribb Fish Inst* 51:404–413
- Magnuson JJ (1978) Locomotion by scombrid fishes: hydrodynamics, morphology, and behavior. In: Hoar WS, Randall DJ (eds) *Fish physiology, vol. 7 locomotion*. Academic Press, New York, pp 239–313
- Manooch CS III, Hogarth WT (1983) Stomach contents and giant trematodes from wahoo, *Acanthocybium solandri*, collected along the south Atlantic and gulf coasts of the United States. *Bull Mar Sci* 33:227–238
- Marsac F, Fonteneau A, Menard F (2000) Drifting FADs used in tuna fisheries: an ecological trap? In: Le Gall JY, Cayre P, Taquet M (eds) *Pêche thonière et dispositifs de concentration de poissons. IFREMER, Actes Colloq.* 28, pp 537–552
- Mauder MN, Harley SJ (2006) Evaluating tuna management in the eastern Pacific Ocean. *Bull Mar Sci* 78(3):593–606
- McBride RS, Richardson AK, Maki KL (2008) Age, growth, and mortality of wahoo, *Acanthocybium solandri*, from the Atlantic coast of Florida and the Bahamas. *Mar Fresh Res* 59:799–807
- Menard F, Fonteneau A, Gaertner D, Nordstrom V, Ste’quert B, Marchal E (2000) Exploitation of small tunas by a purse-seine fishery with fish aggregating devices and their feeding ecology in an eastern tropical Atlantic ecosystem. *ICES J Mar Sci* 57:525–530
- Musyl MK, Brill RW, Boggs CH, Curran DS, Kazama TK, Seki MP (2003) Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data. *Fish Oceanogr* 12:152–169
- Nakano H, Okazaki M, Okamoto H (1997) Analysis of catch depth by species for tuna longline fishery based on catch by branchlines. *Nat Res Inst Bull Far Seas Fish* 24:43–62
- Nakano H, Matsunaga H, Okamoto H, Okazaki M (2003) Acoustic tracking of bigeye thresher shark *Alopias superciliosus* in the Eastern Pacific Ocean. *Mar Ecol Prog Ser* 265:255–261
- Nash A, Whiting J, Luckhurst BE (2002) A pneumatic cradle for handling and tagging wahoo and other large pelagic fishes. *Am Fish Soc Symp* 30:189–194
- Neill WH, Chang RKC, Dizon AE (1976) Magnitude and ecological implications of thermal inertia in skipjack tuna, *Katsuwonus pelamis* (Linnaeus). *Environ Biol Fish* 1:61–80
- NMFS (1999) 1999 Billfish newsletter and cooperative tagging program report. Prepared by David Holtz, Fishery Biologist Southwest Fisheries Science Center, PO Box 271, La Jolla, CA 92038-0271
- Oxenford HA, Murray PA, Luckhurst BE (2003) The biology of wahoo (*Acanthocybium solandri*) in the western central Atlantic. *Gulf Caribb Res* 15:33–39

- Polovina JJ, Hawn D, Abecassis M (2007) Vertical movement and habitat of opah (*Lampris guttatus*) in the central North Pacific recorded with pop-up archival tags. *Mar Biol* 153:257–267
- Rudershausen PJ, Buckel JA, Edwards J, Gannon DP, Averett TW (2010) Feeding ecology of blue marlins, dolphinfish, yellowfin tuna, and wahoos from the North Atlantic Ocean and comparisons with other oceans. *Trans Am Fish Soc* 139:1335–1359
- Schaefer KM, Fuller DW (2002) Movements, behavior and habitat selection of bigeye tuna (*Thunnus obesus*) in the eastern equatorial Pacific, ascertained through archival tags. *Fish Bull* 100:765–788
- Schaefer KM, Fuller DW (2007) Vertical movement patterns of skipjack tuna (*Katsuwonus pelamis*) in the eastern equatorial Pacific Ocean, as revealed with archival tags. *Fish Bull* 105:379–389
- Schaefer KM, Fuller DW, Block BA (2007) Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the northeastern Pacific Ocean, ascertained through archival tag data. *Mar Biol* 152:503–525
- Schuck HA (1951) Notes on the dolphin (*Coryphaena hippurus*) in North Carolina waters. *Copeia* 1951:35–39
- Sepulveda CA, Knight A, Nasby-Lucas N, Domeier ML (2010) Fine-scale movements of the swordfish (*Xiphias gladius*) in the Southern California Bight. *Fish Oceanogr* 19(4):279–289
- Takenaka B, Torricer L, Cooper JC, Pooley, SC (1984) Trends in the market for mahimahi and ono in Hawaii. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent. Admin. Rep. H-84-9, 19 pp
- Theisen TC (2007) Population genetic structure, movement patterns, and environmental preferences of the pelagic wahoo, *Acanthocybium solandri*. Dissertation, Florida Atlantic University
- Theisen TC, Bowen BW, Lanier W, Baldwin JD (2008) High connectivity on a global scale in the pelagic wahoo *Acanthocybium solandri* (tuna family Scombridae). *Mol Ecol* 17:4233–4247
- Uchiyama JH, Boggs CH (2006) Length-weight relationships of dolphinfish, *Coryphaena hippurus*, and wahoo, *Acanthocybium solandri*: seasonal effects of spawning and possible migration in the central North Pacific. *Mar Fish Rev* 68(1–4):19–29
- Viana DL, Hazin FHV, Nunes D, Carvalho F, Vêras D, Travassos P (2008) The wahoo *Acanthocybium solandri* fishery in the vicinity of the Saint Peter and Saint Paul archipelago, Brazil, from 1998 to 2006. *Collect. Vol. Sci. Pap. ICCAT*, 62(5):1662–1670
- Walters V, Fierstine HL (1964) Measurements of swimming speed of yellowfin tuna and wahoo. *Nature* 202:208–209
- Wegner NC, Sepulveda CA, Graham JB (2006) Gill specializations in high-performance pelagic teleosts, with reference to striped marlin (*Tetrapturus audax*) and wahoo (*Acanthocybium solandri*). *Bull Mar Sci* 79:747–759
- Wegner NC, Sepulveda CA, Bull KB, Graham JB (2010) Gill morphometrics in relation to gas transfer and ram ventilation in high-energy demand teleosts: scombrids and billfishes. *J Morph* 271:36–49
- Western Pacific Regional Fishery Management Council (2009) Fishery Ecosystem Plan For Pacific Pelagic Fisheries of the Western Pacific Region. <http://www.wpcouncil.org/documents/FEPs/PacificPelagicFEP/December12005PelagicFEP.pdf>. Accessed 13 Oct 2010