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Original Article

Observations of vertical movements and depth distribution of migrating female lumpfish (*Cyclopterus lumpus*) in Iceland from data storage tags and trawl surveys

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Lumpfish (*Cyclopterus lumpus*) is a high latitude species most abundant in Arctic and sub-Arctic waters of the North Atlantic. Vertical behaviour of this fish is unclear as it is often caught by both pelagic and demersal trawls. To gain greater insight into its behaviour, 41 female lumpfish caught during the Icelandic Groundfish Survey (IGFS) in March were tagged with data storage tags (DSTs); the IGFS finishes ~1 week before the beginning of the lumpfish fishing season (20 March). Data retrieved from returned tags were compared with information on depth and distribution of catches of lumpfish from the IGFS. Thirteen tags were returned with days at liberty ranging from 20 to 61 d. Maximum depth recorded was 308 m (maximum depth of the tag) but based upon interpolation of temperature recordings, one fish may have descended to ~418 m. Lumpfish displayed a range of vertical behaviours termed demersal, surface, and pelagic. During March, most exhibited either demersal or pelagic behaviour but the time spent in surface behaviour increased from March to April. During demersal behaviour, depth was rarely constant indicating the fish were not stationary. Both DST and catch data from the IGFS indicate that lumpfish exhibit diel patterns in vertical behaviour. As lumpfish frequently exhibit demersal behaviour, the use of the IGFS to monitor changes in abundance is justified. As lumpfish spend a significant amount of time in both the pelagic and demersal zone, they should be considered as a semi-pelagic (or semi-demersal) fish during this life stage/time of year.

Keywords: archival tags, lumpsucker, spawning migration, temperature, vertical movements.

Introduction

Lumpfish (*Cyclopterus lumpus*) is a high latitude species most abundant in Arctic and sub-Arctic waters of the North Atlantic. Adult fish are found in coastal waters in substantial numbers only during spring and summer when they come to spawn. It is during this time at the coast that they are targeted by fishers. Lumpfish have characteristics which indicate that they may be a demersal species, i.e. pelvic fins which have evolved into a suction disc and the lack of a swimbladder. However, they have evolved features, such as an almost uncalcified cartilaginous skeleton, which brings them close to neutral buoyancy, indicating the potential for a pelagic lifestyle (Davenport and Kjørsvik, 1986).

There are many conflicting reports concerning the behaviour and vertical distribution of lumpfish. Based on catch data, Cox and Anderson (1922) concluded that lumpfish are semi-pelagic rather than a strictly bottom or shore fish. Discounting the early description by Cox and Anderson, Wheeler (1969) describes it as primarily a bottom dwelling fish. However, Wheeler (1978) does mention that many of the non-breeding adults live "bathypelagically". There are many reports which describe the catches of lumpfish in pelagic trawls (Holst, 1993; ICES, 2012; Eriksen *et al.*, 2014). Both Schultz (1981) and Blacker (1983), when discussing catches of lumpfish in the Norwegian Sea and various areas in the Northeast Atlantic respectively, state that the majority of lumpfish were caught in the upper 60 m of the water column. Any fish caught when trawling deeper than 60 m were attributed to capture during shooting and hauling of the net (Blacker, 1983). Detailed in-trawl imaging of pelagic tows confirm that the majority of lumpfish are caught in the upper 60 m, although fish caught deeper than 60 m were not uncommon with one fish entering the net at a depth of 156 m (Rosen and Holst, 2013, Rosen *et al.*, 2013, S. Rosen, pers. comm.). Blacker (1983) stated that catches of lumpfish in bottom trawls were a rare occurrence. However, this is not as unusual as claimed by Blacker (1983) as lumpfish are frequently caught in bottom trawl surveys around Iceland, Newfoundland and in the North Sea and the Barents Sea (Knijn *et al.*, 1993; Casey and Myers, 1998; Wienerroither *et al.*, 2013; Marine Research Institute, Iceland (MRI), unpublished data) which adds to the confusion about their behaviour.

While pelagic and demersal trawl surveys can give insight into vertical depth distribution at the population level, they cannot give information on the movement of individual fish. Data from trawl surveys are thus unsuitable to identify whether a single fish utilizes only a small proportion of the species depth distribution or if it moves through the entire depth range in which the species is caught. Trawl surveys are also limited at the temporal scale, with surveys typically lasting only for a few weeks each year, while depth distribution may change during the year. With developments in data storages tags (DSTs), it is possible to gain greater insight into the behaviour of many fish species. DSTs can record vertical movements at a resolution of seconds and can potentially provide data gathered over several years (Grabowski *et al.*, 2014).

This study investigates the vertical swimming activity of lumpfish in Iceland during its migration from open water to coastal areas for spawning using DSTs. Catch data and depth distribution from the IGFS were compared with the data from the DSTs. Doubts have been raised by Icelandic fishers over whether data from a groundfish survey is appropriate for lumpfish assessment when it is believed to be semi-pelagic. This question is addressed in context of the results from this study. The optimum balance between the frequency of depth recordings, and total recording time when tagging lumpfish with DSTs, is also considered. This paper does not discuss the horizontal movements of the fish with regards to their migration as this is addressed in greater detail along with other tagging data in Kennedy *et al.* (2015).

Material and methods

Data storage tags

Forty-one female lumpfish between 34 and 46 cm were tagged aboard RV Bjarni Sæmundsson during the IGFS in March 2013 (20 fish) and 2014 (21 fish) (Figure 1) . These fish were caught by bottom trawl with tow duration of 1 h. All tagged fish were likely to be mature and close to spawning as >99% of the female lumpfish caught during the IGFS are mature (MRI, unpublished data). After capture, the fish were placed in a tank with flow through seawater. Only fish which did not show signs of damage such as floating or bleeding were tagged. Total length was measured for each fish and the tag attached using stainless steel wire threaded through the dorsal hump (Figure 2); the fish were not anaesthetized during this process. After tagging, the fish were returned to the tank and if deemed to be in good health, released. Previous tagging experiments on lumpfish in Iceland indicate a high recapture rate (23%) of fish tagged with Peterson disc tags during the IGFS in the fishing seasons which starts soon after the survey (Kennedy *et al.*, 2015).

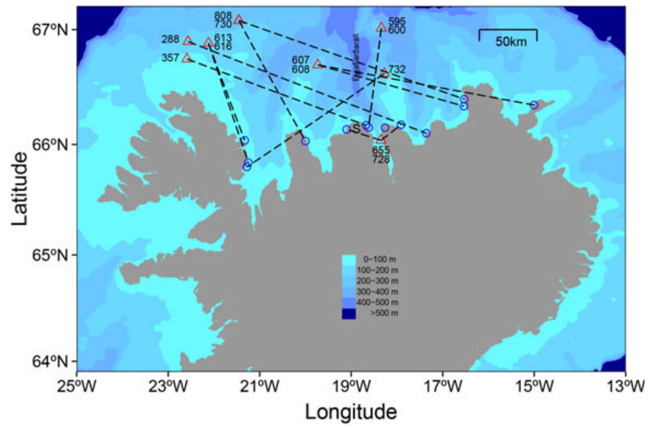

Figure 1. Map of Iceland showing the tag number, release site (triangles), and recapture site (circles). Location of Siglufjörður is marked with S. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Figure 2. Lumpfish tagged with a DST. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

The tags used in this study were DST milli-L and DST micro-TD (Star Oddi Marine Device Manufacturing) capable of recording temperature in the range of −1.0 to 40.0°C (±0.1°C). The milli-L tags, which weigh 5 g in water, were calibrated to 250 m and had an accuracy of ±2.0 m. The micro-TD tags, which weigh 1.9 g in water, were calibrated to 300 m and had an accuracy of ±1.5 m. The typical weight of the size range of the fish tagged (the tagged fish were not weighed) is between 2 and 5 kg (MRI, unpublished data) thus a milli-L tag on the smallest fish would amount to <1% of the fish's weight. As this was the first study of lumpfish using DSTs, a variety of recording sequences were programmed (Supplementary Table S1). Depth was collected at intervals from 20 s to 5 min and temperature from 1 to 9 min until the end of May when the tag would switch to hourly recordings, continuing until the memory was full on approximately March the following year.

Displacement distance, the distance between release and recapture, was calculated using Google Earth (http://www.google.com/earth/) and was defined as the shortest distance between the two points without crossing land. Average depth for each hour was calculated using all the depth measurements for that hour. The average depth and the changes in depth over time were used to interpret the behaviour of the fish. Behaviour for each hour was classified into three types (Figure 3):

(1) surface behaviour, where average depth for that hour was <20 m,

(2) demersal behaviour (where the fish is likely to be spending a significant amount of time close to the seabed), when the average depth for an hour does not change by >10 m in either of the two previous average hourly depths,

(3) pelagic behaviour (where the fish is spending a significant amount of time within the water column), behaviour which did not fit the description of surface or demersal behaviour.

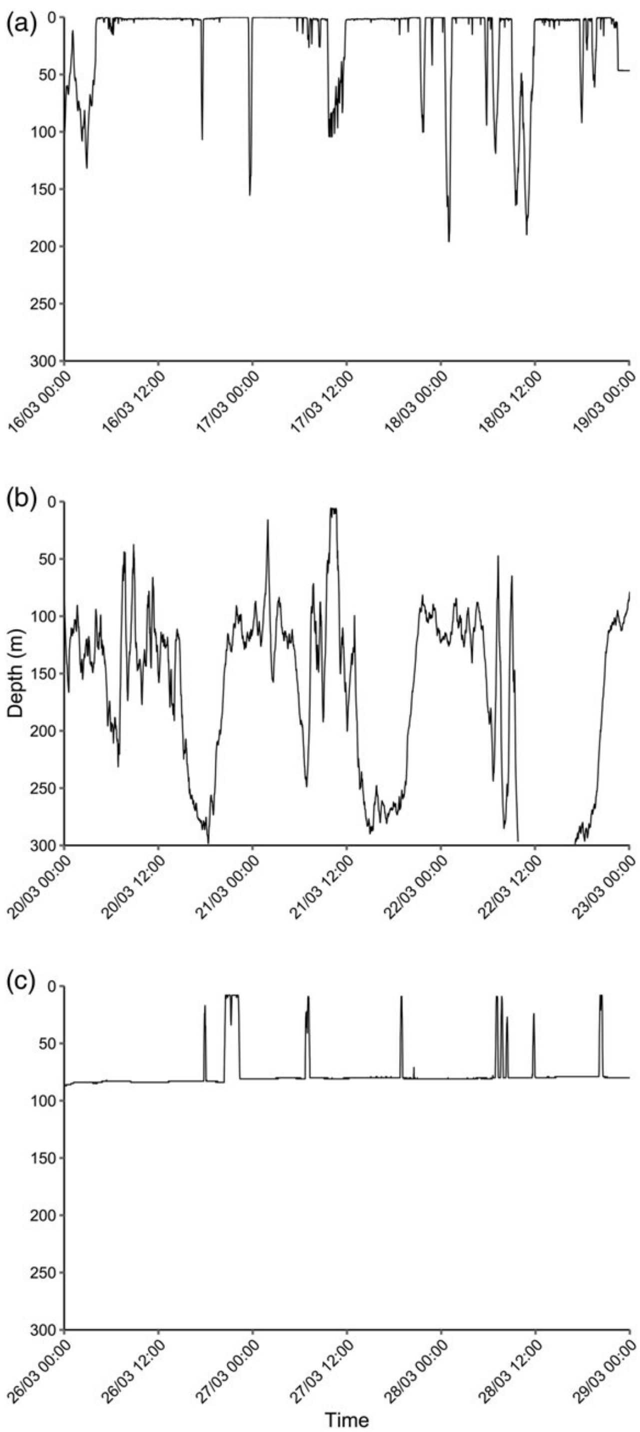

Figure 3. Depth time plots from three lumpfish showing examples of the three behaviour types identified as (a) surface (608), (b) pelagic (600), and (c) demersal (607).

The percentage of time spent in each behaviour type for each month was estimated and the differences compared using a two-way analysis of variance (ANOVA) with month and individual fish as factors.

As the fish were migrating through areas of continuously changing depth, the bottom depth was unknown. This made it difficult to estimate whether the fish exhibited a diel pattern in vertical behaviour or had moved into an area of shallower/deeper water. Thus, to determine if a diel pattern in vertical behaviour existed, a difference in the average depth during the day and during the night was tested using a *t*-test. To avoid confounding factors such as a change from demersal/pelagic to surface behaviour the period for each fish was split, with weeks when surface behaviour exceeded 25% (see below) being analysed separately. If the fish made an obvious move from deep to shallow water, e.g. fish 595 and 607 (Supplementary Figure S1), then the period in shallower water was analysed separately from the period in deeper water. The day-to-day location of each fish was not known, thus day and night were defined by the time of sunrise and sunset in Siglufjörður, a town in northern Iceland which is approximately centre in the distribution of release/recapture locations (Figure 1). Sunrise and sunset differed by 15 and 3 min between Siglufjörður and the most western and most northern release location respectively; this was considered to have an insignificant effect on the results. A value of 25% for the amount of time spent in the upper 20 m during a week was used to separate demersal/pelagic behaviour from surface behaviour. The justification for this is that preliminary analysis of the data showed that 74% of the values for the amount of time spent in the upper 20 m was <20% while 23% of the values were >30%, i.e. it was rare for fish to spend between 20 and 30% of time in the upper 20 m. Therefore, we used a value of 25% to separate the two types of behaviour.

Maximum descent and ascent rates were calculated for each fish for the duration of the entire ascent/descent, i.e. from when depth begins to increase/decrease until depth ceases to increase/decrease. Ascent/descent rates were expressed as both cm per second and body lengths s^{-1}, body length being the length of the fish when tagged (Table 1).

The impact of using different recording intervals on the total vertical range and the depth–time profile was investigated using the six fish recaptured in 2013. A recording interval of 1, 3, 5, 10, 20, 30, and 60 min was simulated using the 23 h periods when a 20 s recording interval was used. Using the data from these periods, the vertical range (max–min depth recorded) was calculated for each of these simulated recording intervals and an average vertical range was estimated for each recording interval length. Analysis of covariance (ANCOVA) was used to test for the effect of the length of the recording interval on the average estimated vertical range with recording interval as the covariant and individual fish as the factor.

Survey data

Using data on catches of lumpfish from the spring IGFS, depth distribution, and the possibility of diel patterns in vertical behaviour was investigated. The IGFS has been carried out every year in

Table 1. Details of the recaptured fish with tag type, date released, TL, DAL, displacement distance (Dist), maximum depth recorded (D. max), and maximum vertical range in 1 d.

Fish	Type	Date	TL (cm)	DAL	Dist (km)	D. max (m)	Range (m)
595	Milli	13.3.2013	44	26	97	250	247
600	Milli	13.3.2013	41	26	97	308 (418)	298
607	Milli	14.3.2013	41	33	147	303 (498)	300
608	Milli	14.3.2013	40	20	215	244	244
613	Milli	17.3.2013	36	33	123	283	199
616	Milli	17.3.2013	39	23	101	189	155
655	Milli	2.3.2014	40	60	44	239	188
728	Milli	2.3.2014	36	38	33	233	233
730	Milli	6.3.2014	34	33	134	284	281
732	Milli	3.3.2014	37	36	163	308	177
808	Milli	6.3.2014	39	54	230	278	278
288	Micro	7.3.2014	42	48	248	309	309
357	Micro	6.3.2014	38	61	186	172	172

Value in brackets is maximum depth inferred from temperature recording.

Table 2. Average (A) and standard deviation (SD) of the proportion of behaviour classified into the three behaviour types, demersal (D), pelagic (P), and surface (S) in each month.

	Demersal		Pelagic		Surface	
	A	SD	A	SD	A	SD
March	36	20	55	17	9	9
April	32	21	39	12	29	17
May	9	–	15	–	76	–

Data were only available for one fish in May.

March since 1985. This survey covers the shelf around the entire coastal area of Iceland down to a depth of ~500 m and consists of 500–600 stations per year. Fishing occurs over a 24 h period and the numbers of male and female lumpfish caught are counted. Trawling is carried out using a Granton trawl with tow duration of 1 h and tow speed of 3.8 knots. Full details of this survey are available in English (MRI, 2010).

Results

Data storage tags

Thirteen-tagged lumpfish were recaptured at the time of writing, six in 2013 and seven in 2014, with days at large (DAL) between 20 and 61 d (Table 1). The fish exhibited a displacement distance from 33 to 248 km (Figure 1; Table 1). For every tag returned, the data showed the fish initially descended through the water column upon release. There was no obvious difference in behaviour of each fish in the first 24 h compared with other recording periods. Thus, the fish was assumed to resume normal behaviour after their initial descent, and data recorded between release and the end of the initial descent was removed. The greatest depth recorded was 309 m (fish 288), recorded by a micro tag calibrated to 300 m with ± 2 m accuracy. Daily, all fish would ascend and descend through the water column, regularly covering a vertical range of >100 m over 1 d and up to a maximum of 309 m (Supplementary Figure S1 and Table 1). Average ascent and descent rates were not significantly different (t-test, $t = 0.226$, d.f. $= 23.794$, $p > 0.05$). Descent rates of up to 21 cm s^{-1} or 0.53 body lengths s^{-1} and ascent rates of up to 20 cm s^{-1} or 0.56 body lengths s^{-1} were recorded.

Two fish (fish 600 and 607) spent several hours below the depth range of their tags. The tags, which were calibrated to 250 m, recorded a maximum depth of 302 and 303 m which represents the deepest the tag was able to measure (B. Sigurgeirsson, Star Oddi, pers. comm.). The depth recorded by the tag then remained unchanged for several hours. From the data for fish 600, temperature was negatively correlated with depth, and when the tag registered a depth of 302 m, temperature continued to fluctuate and on most occasions, would continue to decrease indicating the fish descended deeper than 302 m. During one dive, when the tag first recorded a depth of 302 m, the tag recorded a temperature of 1.7°C, over the next 27 min, the temperature continued to decrease reaching a minimum of 0.5°C. During this dive, there was a significant linear correlation between depth and temperature between 150 and 302 m ($R^2 = 0.996$), if the correlation between temperature and depth remained linear until 0.5°C, then this means that fish 600 reached a depth of 418 m. The descent from 302 to 418 m, in 27 min, is equivalent to a descent speed of 7.2 cm s^{-1}. Based upon results above, this is within the capabilities of lumpfish. A similar situation (but relating to an ascent) was seen for fish 607 where there was a significant linear correlation between depth and temperature between 230 and 303 m ($R^2 = 0.954$). The recorded temperature showed an increase from 2.7 to 3.4°C with no change in the maximum depth of 303 m. This indicates the fish ascended from a depth of 498 m. An ascent from 498 to 303, in 18 min, is equivalent to an ascent speed of 18.1 cm s^{-1}. This is also within the recorded capabilities of lumpfish. Both of these deep recordings were recorded on 18.03.2013 and are likely to be associated with the Eyjafjarðaráll (Figure 1), a deep underwater canyon on the northern Icelandic shelf in which both fish will have been close to, given their release and recapture locations. Two other fish reached the maximum limit of their tag (fish 732 and 288, Table 1). However, this depth was only recorded once, and the following recording showed that they had ascended back into the working range of the tag.

The time spent in each behaviour type varied over time (Table 2). During March, all fish spent the majority of their time either in demersal or pelagic type behaviour. The average time spent in surface behaviour increased significantly from March (9%) to April (29%) (two-way ANOVA: d.f. $= 1$, $F = 10.93$, $p < 0.0001$). The surface behaviour for the one fish which was at liberty until May also showed an increase in surface behaviour from April to May (Table 2).

The average depth during the day was significantly greater than during the night for 11 of the 13 fish for at least one of the analysed periods indicating a diel pattern in vertical behaviour (Figure 4). For only one fish was the average depth greater during the night than during the day (fish 730) (t-test: $t = -15.113$, d.f. $= 4082.8$, $p < 0.0001$) and for one fish there was no significant difference (fish 808) (t-test, $t = 2.1064$, d.f. $= 7920.7$, $p > 0.05$). Diel patterns in vertical behaviour occurred when the fish were displaying both demersal/pelagic behaviour and surface behaviour. During pelagic/demersal behaviour, the fish would be at shallower depths during night (Figure 5). During surface behaviour, fish tended to dive deeper during the night than during the day but the pattern was not as clear as during demersal/pelagic behaviour (Figure 5). Diel patterns in vertical behaviour were not exhibited throughout the entire recording period for every fish. For example, a diel patterns was present in fish 595 while at depths of >250 m, but this was not evident after moving into shallower depths (100–200 m). However, after switching to surface behaviour, a diel pattern resumed (Figure 4, Supplementary Figure S1).

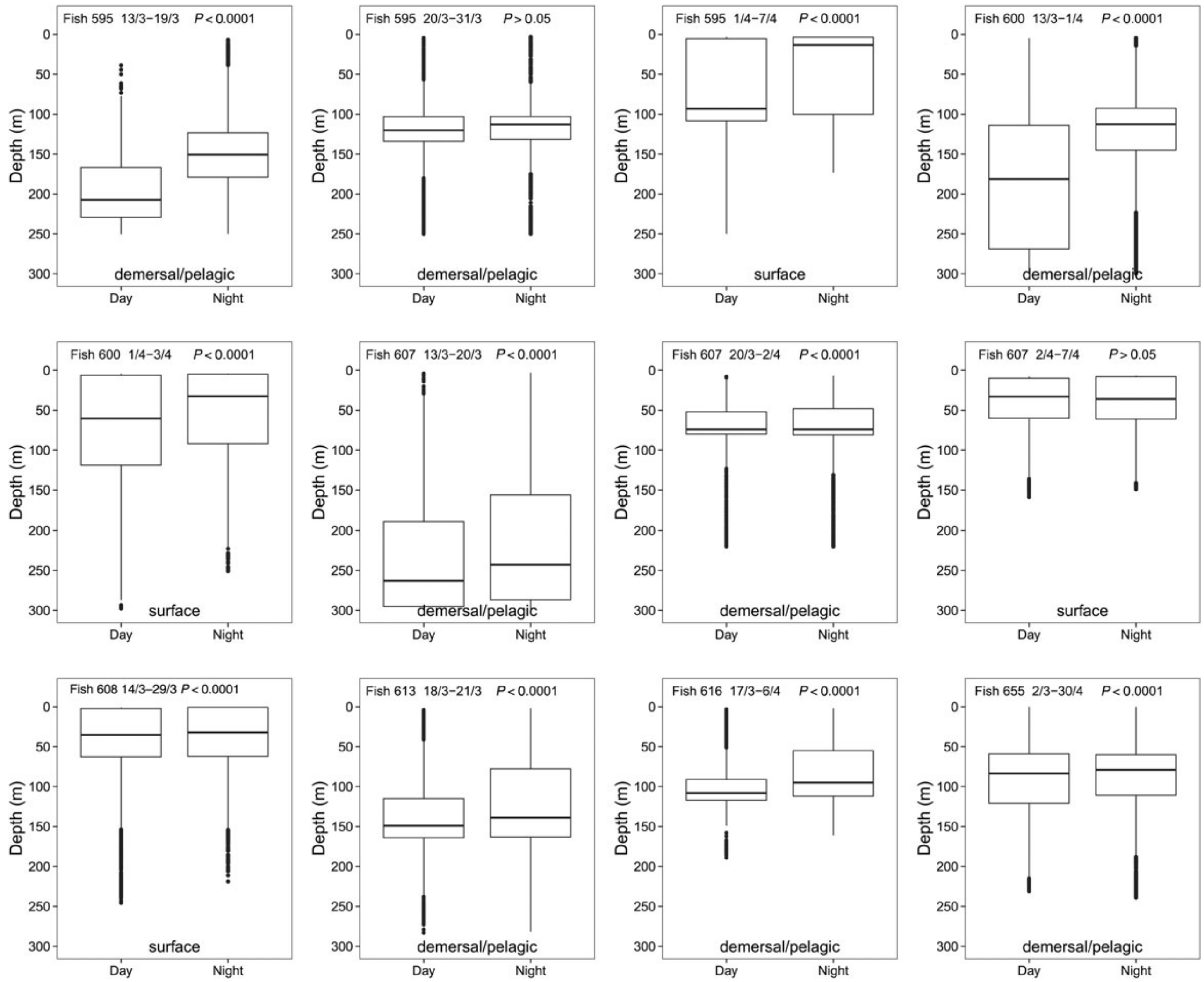

Figure 4. Box plots of depth for each fish during the day and night during specific periods with labels showing *p*-value of the *t*-test of the difference in average depth during day and night and behaviour type during the period in question.

During demersal behaviour, depth was continuously changing suggesting that the fish were actively swimming close to the seabed. Continuous movement is also supported by the lack of a tidal signal in the depth recordings. Tidal signals were clearly discernible when the fish were caught in the net (Figure 6), indicating that when the fish are relatively still, a tidal signal would be evident. Close to the time when they were caught, two fish did appear to remain still for significant amount of time (616 and 730), with a visible tidal signal, followed by ascents to the upper 10 m then descents to a similar depth. They then remained stationary again, before being hauled to the surface.

The DSTs showed that lumpfish, during their time at liberty, experienced temperatures between 0 and 6°C with the majority of measurements being between 1.5 and 4°C (Figure 7). Two fish experienced higher temperatures compared with the other fish (fish 613 and 616) (Figure 7, Supplementary Figure S1). Fish 288 showed an increase between the temperature experienced during its first 9 DAL (mean = 2.4°C, s.d. = 0.24) and the temperature experienced the following 6 d (mean = 3.8°C, s.d. = 0.71) (Supplementary Figure S1). This elevation can also be seen in the data from fish 357, but the rise is not as great (7.3.14–12.3.14, mean = 2.1°C, s.d. = 0.14; 12.3.14–20.3.14, mean = 2.6°C, s.d. = 0.24) (Supplementary Figure S1). Temperature was generally negatively correlated with depth but this was not always the case, as the recordings from some fish indicated that surface waters were colder (Supplementary Figure S1).

With decreased frequency of recordings, there was a significant decrease in the average estimated vertical range (ANCOVA; $F = 56.38$, $p < 0.001$) (Table 3). Examining the effect of recording intervals on the time–depth plots show that, on a scale of 1–2 h, there is very little difference between a recording interval of 20 s and 1 min (Figure 8a). When an interval of 20 s was used, 98% of the changes in depth between recordings were <2 m. When examining the movements over a 24 h period, fewer ascents and descents within the water column were apparent when a greater interval between recordings was used (Figure 8b).

Survey data

During the IGFS, lumpfish are primarily caught at depths between 40 and 500 m, with 95% being caught shallower than 244 m and 99% being caught shallower than 296 m (Figure 9). The deepest depth in which a lumpfish was caught was 512 m. Ninety-nine per

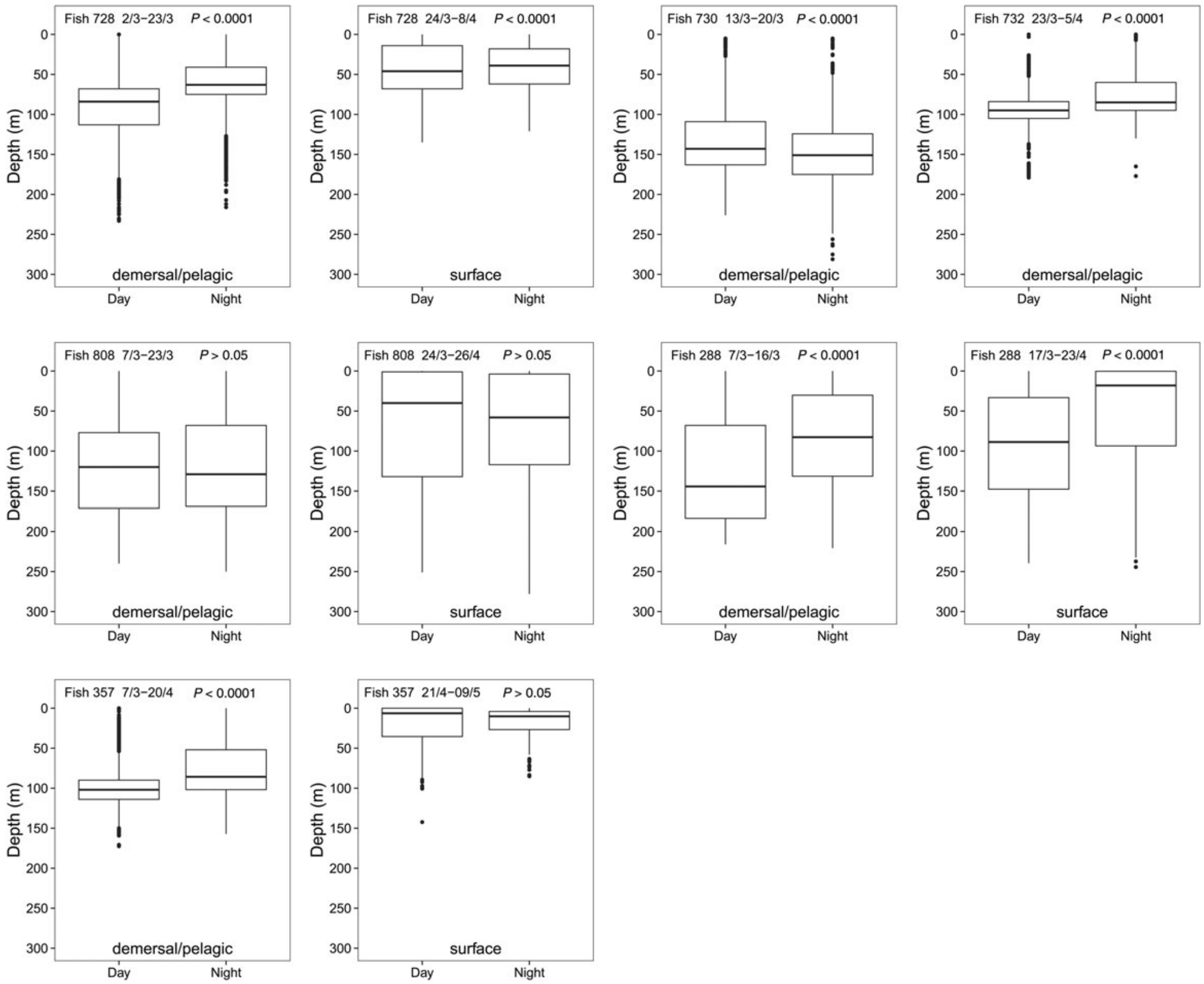

Figure 4 Continued

cent of the stations in the IGFS are shallower than 437 m (Figure 9). The number of lumpfish caught peaked during the daylight hours and decreased at night (Figure 10).

Discussion

This is the first study to employ DSTs to investigate the behaviour of lumpfish and to reveal that they spend a significant amount of time moving vertically through the water column. These ascents and descents were substantial, with daily vertical ranges of over 100 m being common. There is a consensus that the vertical movements of pelagic fish through the water column are linked with feeding (Hays *et al.*, 2009; Weng *et al.*, 2009; Dewar *et al.*, 2011; Armannsson and Jónsson, 2012). As the stomachs of lumpfish caught during the IGFS contain large amounts of water and food (Kennedy, pers. obs.), it seems likely that the vertical movements seen in lumpfish are also related to the search for prey.

The lack of a discernible tidal cycle in the depth recordings and the fact that depth is rarely constant over time indicate that the lumpfish were seldom stationary during their time at liberty. As these fish were tagged during their spawning migration, this is unsurprising. It could be argued that the tags were not sensitive enough to pick up the tidal signal. However, this signal is clear when they are caught in gillnets and are unable to make large depth changes. Two fish (616 and 730) were inactive for short periods before becoming active again; this was evident from the visible tidal signal in the depth recordings. This period of inactivity was likely to be due to the fish being caught in a gillnet then subsequently disentangling themselves. In the few hours leading up to their inactivity, the maximum depth recorded was deeper than the depth where the inactivity took place, this indicates that the fish was likely to be within the water column. In combination with the fact that fish 616 was subsequently captured in a gillnet and hauled to the surface, it is more likely that they were caught in a gillnet rather than simply sitting on the bottom. This indicates that lumpfish are capable of freeing themselves from gillnets. As lumpfish have tough skin and lack scales, they are less likely to be damaged by the net compared with other species, and results from tagging studies, which used gillnets (Kennedy *et al.*, 2015), show that they are capable of surviving this experience. Fish 730 appears to get caught in a net on the 17.3.13, 3 d before the start of the lumpfish fishing season so this is likely to have been in a gillnet used for targeting cod.

Both the trawl and DST data support the hypothesis that lumpfish exhibit a diel pattern in vertical behaviour. These data are in

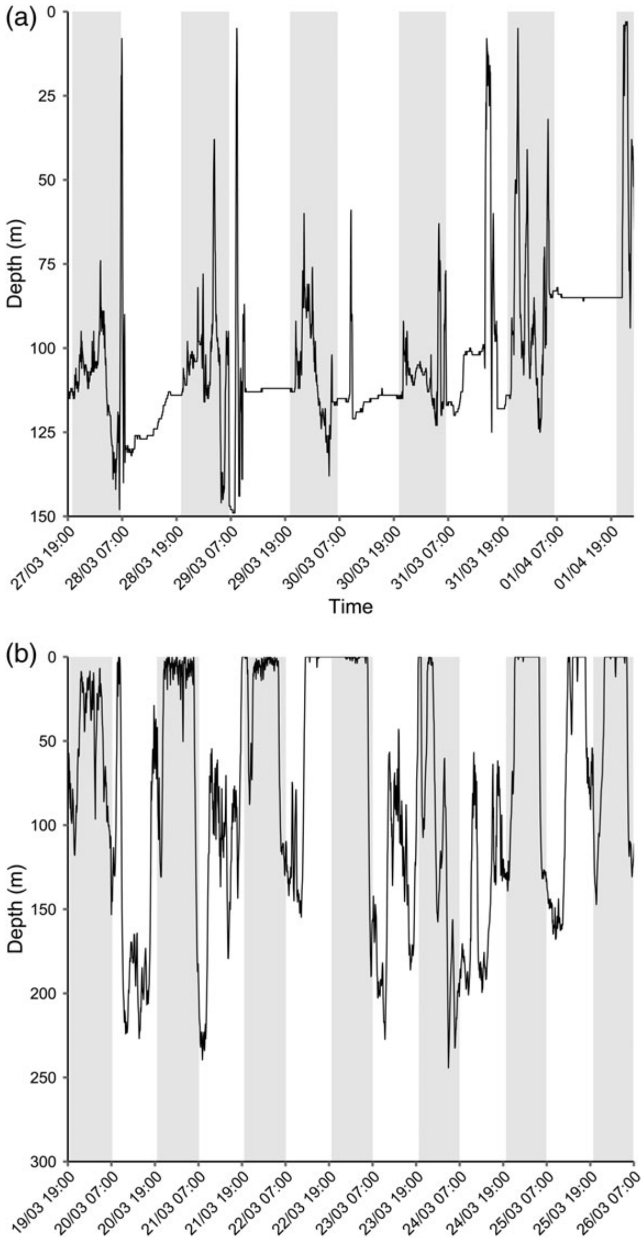

Figure 5. Depth – time plots of fish (a) 616 and (b) 288 showing diel patterns in vertical behaviour during demersal/pelagic and surface behaviour respectively. Shaded area marks time between sunset and sunrise. Note differing scales on *x*-axis.

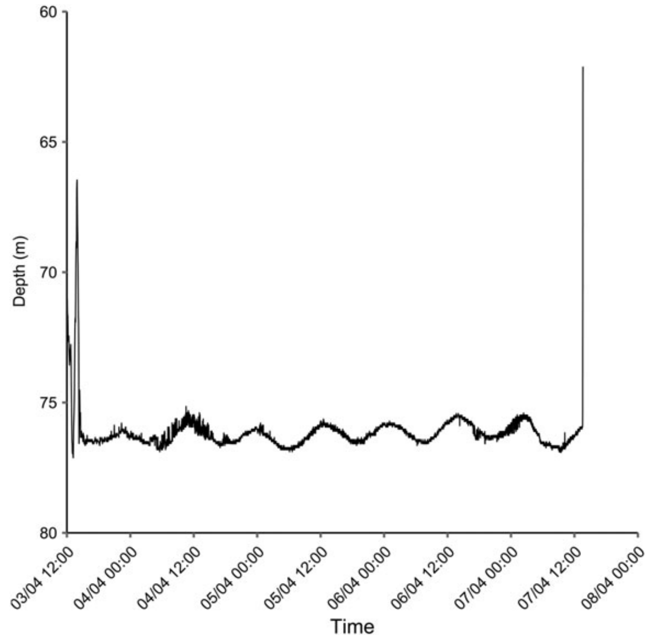

Figure 6. Depth time plot for fish 600 with the evident tidal cycle when caught in a gillnet.

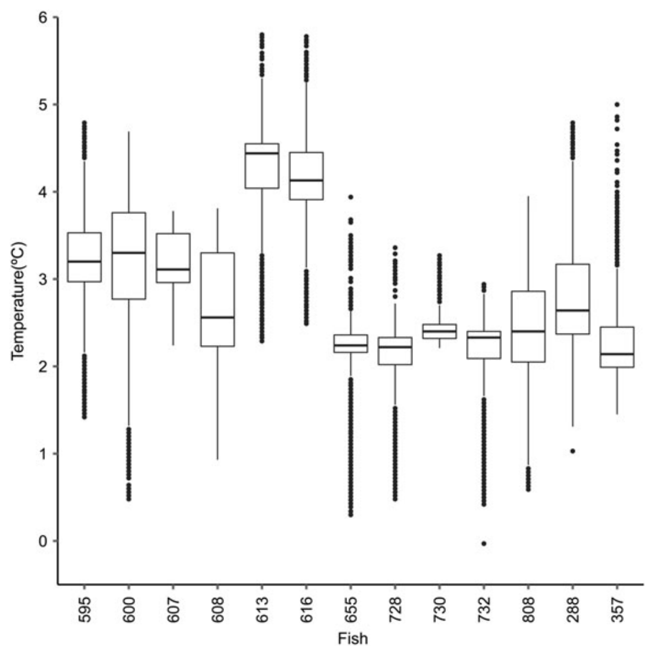

Figure 7. Box plots of temperatures recorded by the DST for each lumpfish.

agreement with the bottom trawl data from Newfoundland and Labrador which show that lumpfish catchability is higher during the day than at night (Casey and Myers, 1998). The current study shows that this is related to a diel pattern in vertical behaviour and not related to lumpfish reacting to the trawl. Eleven of the 13 fish were found to be significantly deeper during the day than at night. This diel pattern was more prominent when the fish were carrying out demersal/pelagic behaviour as opposed to surface behaviour.

A variety of species exhibit a diel pattern in vertical behaviour which is generally linked to movements of their prey. Ocean sunfish have a similar diet to lumpfish (gelatinous zooplankton) (Davenport, 1985; Nakamura and Sato, 2014), and also exhibit diel pattern in vertical behaviour (Potter and Howell, 2011). However, the diel pattern of lumpfish is not as pronounced as seen in ocean sunfish. This is because ocean sunfish come to the surface to rewarm after feeding in deep water (Nakamura *et al.*, 2015). The DST tags show that surface waters around Iceland are not necessarily warmer than deep water, thus there would be little advantage for lumpfish to move up into surface waters regularly. The pattern in vertical behaviour of lumpfish was not as consistent across individuals as seen in other pelagic fish (Hays *et al.*, 2009;

Table 3. Depth range for each fish on the (a) 18.03.13, (b) 27.03.13, and (c) 10.04.13 based upon different recording intervals of the DST.

		Recording interval (min)							
Fish	**Date**	**0.3**	**1.0**	**3.0**	**5.0**	**10.0**	**20.0**	**30.0**	**60.0**
595	a	213	212	211	212	182	182	168	146
595	b	178	178	174	173	173	166	133	116
600	a	298	298	297	297	296	294	296	235
600	b	261	261	261	261	261	261	261	261
607	a	200	200	200	185	185	185	156	156
607	b	72	72	72	72	62	60	62	1
607	c	109	108	108	104	104	104	96	96
608	a	195	194	194	191	191	191	191	191
608	b	61	61	60	60	60	60	59	58
613	a	188	187	187	187	185	182	182	181
613	b	140	138	123	121	121	114	114	113
616	a	156	155	154	155	155	152	140	122
616	b	142	142	142	142	142	141	142	140
Mean		170	170	168	166	162	161	154	140
% diff			0	1	2	5	5	9	18

Mean for each recording interval is shown as well as the percentage difference between the mean and the mean from a recording interval of 0.3 min.

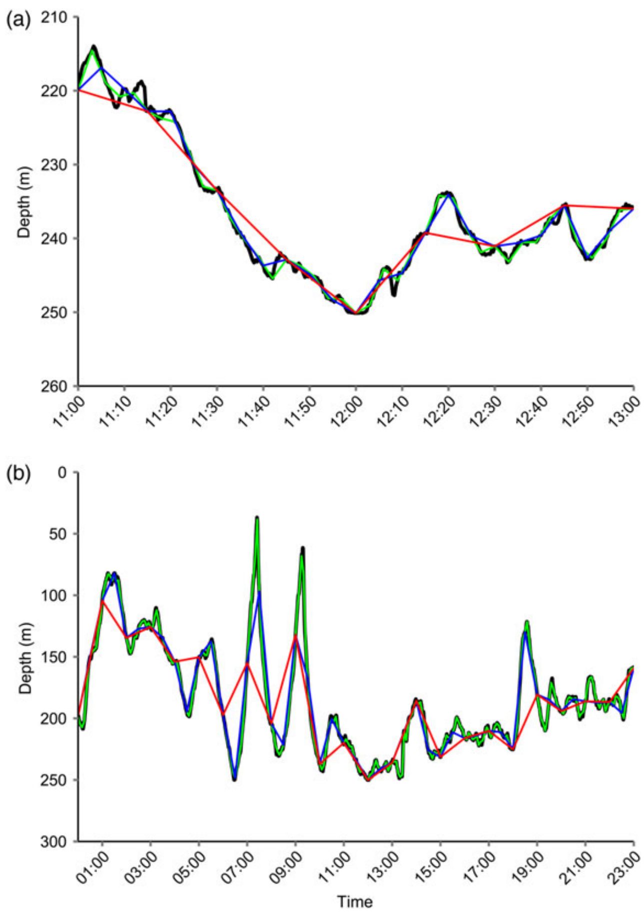

Figure 8. Depth time plot for fish 595 on the 18.03.2013 with recordings taken at intervals of (a) 20 s (black, the original resolution) and 3 (green), 5 (blue), and 10 (red) minute intervals and (b) 20 s (black) and 5 (green), 30 (blue), and 60 (red) minute intervals. Note differing scales on *x*- and *y*-axis.

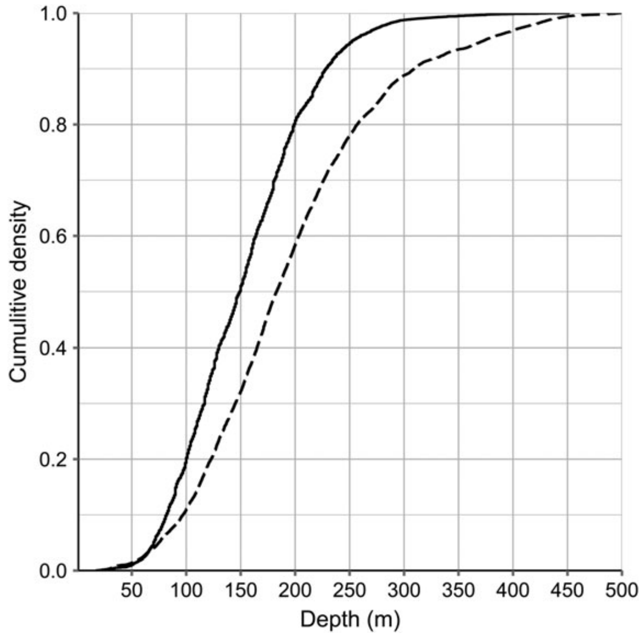

Figure 9. Cumulative density of catches of female lumpfish (solid) and number of stations (dashed) vs. depth for the Icelandic groundfish survey (IGFS) in Spring from 1985 to 2014.

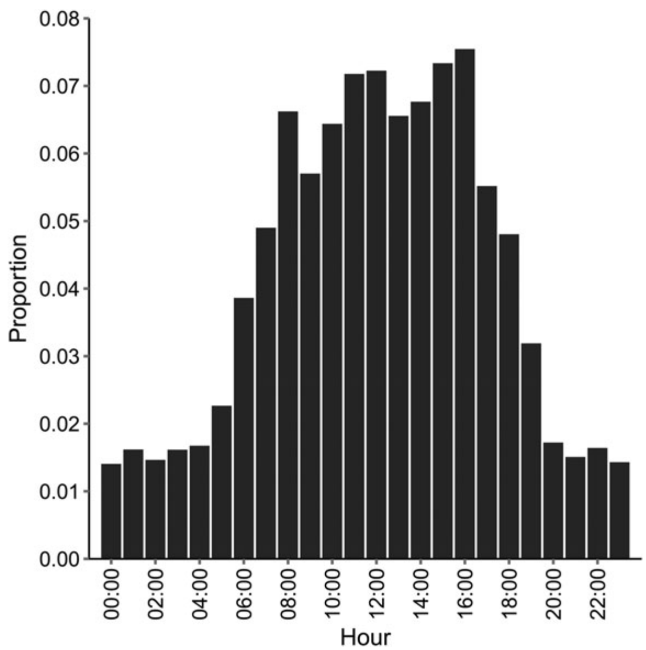

Figure 10. Proportion of total number of lumpfish caught during the Icelandic groundfish survey (IGFS) from 1985 to 2014 by hour.

Weng *et al.*, 2009; Dewar *et al.*, 2011). This may be because the diet of lumpfish is diverse, consisting of both pelagic and benthic organisms (Davenport, 1985), thus they may feed on prey which does and does not exhibit diel patterns in vertical behaviour. Local site-specific conditions such as bathymetry and currents may also affect diel patterns. Similar variability is seen in other species, such as the Pacific cod (*Gadus macrocepahlus*), where some individuals alternate between being deeper during day and deeper during night (Nichol *et al.*, 2013) so this variability in lumpfish is not unusual.

Lumpfish spent greater amounts of time exhibiting surface behaviour in April compared with March. During surface behaviour, diel patterns in vertical behaviour were less pronounced, with differences in average depth between night and day being less than during demersal/pelagic behaviour, but several fish did tend to dive to greater depths during the day than during the night. The reason for this increase in surface behaviour is unclear, it may be related to them being closer to shore in April than in March. However, fish 655 and 728 were tagged in the coastal area, but fish 655 did not exhibit surface behaviour at any time and fish 728 did not exhibit surface behaviour until 25th March. A link to feeding, or more precisely, the lack thereof, could be another explanation for the increase in surface behaviour. Stomachs of lumpfish caught in coastal waters have much less food than fish caught during the IGFS (Kennedy, pers. obs.), or tend to be devoid of food (Cox and Anderson, 1922; Davenport, 1985), which suggests feeding activity is reduced when in coastal waters.

In March, lumpfish are primarily caught at depths <300 m (present study) which explains why the depth range of the tags (milli-L: 250 m, micro-TD:300 m) was rarely exceeded. However, there are some areas over the northern Icelandic shelf which exceed 400 m and two lumpfish appeared to have dived deeper than this (based on temperature recordings). The inferred depths of the two fish which descended below the depth range of their tags are considered plausible based upon their ascent and descent speed and there is an area close to where these fish were released which is of this depth.

The current study shows that lumpfish will move through the entire water column, from the upper few metres down to a depth of over 400 m during spring. This is in contrast to previously published reports of the depth distribution of lumpfish which state that lumpfish are found primarily in the upper 60 m of the water column (Schultz, 1981; Blacker, 1983). Detailed in-trawl imaging of pelagic tows during May 2012, July 2012, and November 2011 in the Norwegian Sea confirm that the majority of lumpfish caught are caught in the upper 60 m, however, fish caught deeper than 60 m are not uncommon (Rosen and Holst, 2013; Rosen *et al.*, 2013; S. Rosen, pers. comm.). The reason for this is at these times of the year, lumpfish will not be migrating, whereas in the present study, the fish are migrating from the feeding areas to coastal spawning areas so it is unsurprising that they behave differently.

Throughout their time at liberty, the temperature range experienced by fish 613 and 616 was significantly higher than that experienced by the other fish. These fish were released in an area where Atlantic water from the south flows by the west of Iceland and the Vestfirðir peninsula onto the North Icelandic shelf (S. Jónsson, University of Akureyri, pers. comm.). A temperature elevation can also be seen in the temperature–time profile of fish 288 and 357 on the 18–21.03.2013, which is likely to be related to these fish passing through this same flow of Atlantic water.

Fishing for lumpfish in Iceland is limited both by their arrival at the coast and regulatory restrictions. In general, the targeting of lumpfish is only permitted during ~15 weeks of the year, thus the majority of tags will be expected to be returned within this period. A preliminary study in 2012 tagged 94 fish with Peterson tags during the IGFS and achieved a return rate of 23% within two months of tagging, but to date, no other tags were returned after those first two months (Kennedy *et al.*, 2015). Of fish tagged during the fishing season, only ~0.8% of tags were returned after more than 250 d at liberty; however, this low return rate is likely to have been affected by rusting of the nickel pins (Fréchet *et al.*, 2011; Kasper *et al.*, 2014; Kennedy *et al.*, 2015). This indicates that it is unlikely for DSTs to be returned after the forthcoming fishing season has ended. It is thus prudent, when programming the DSTs, that priority should be placed on recording frequency as opposed to total recording time. However, increasing the recording frequency to <5 min intervals between recordings would not be of great benefit. When considering movements at the scale of weeks, increasing the recording interval to 5 min led to only a 2% drop in the recorded vertical range compared with an interval of 20 s. Thus, for the present study, increasing the shortest interval between recordings to 5 min would not have had a significant impact on the results while allowing for an increase in the recording period.

Total allowable catch advice for the Icelandic lumpfish fishery is based on a biomass index from the IGFS. This has been criticized as lumpfish are believed to be semi-pelagic, and many fishers believe that lumpfish spend most of their life at the surface (Bogason, 2014). The present study shows that lumpfish spend an increased amount of time at the surface when they reach coastal areas, and are targeted using gillnets by fishers, which may explain this opinion on the behaviour of lumpfish. As lumpfish frequently exhibit demersal behaviour, the use of the IGFS to monitor changes in population abundance and to issue management advice based on data from the IGFS is justified. However, as lumpfish also spend a significant proportion of time in the water column thus the biomass index from the IGFS should be regarded as a relative rather than an absolute estimate of spawning-stock biomass. Due to the small sample size of the present study, it is difficult to get a reliable estimate of the proportion of time spent in the demersal zone. It is therefore, currently not possible to extrapolate the biomass index from the IGFS to total abundance of lumpfish around Iceland.

In conclusion, it is clear that lumpfish are a mobile fish making large ascents and descents throughout the entire water column. They spend a significant amount of time associated with both the seabed and ocean surface. The time associated with the sea surface increases from March to April. Lumpfish display a range of vertical behaviours, often exhibit diel vertical migration and spend an increasing amount of time in the upper 10 m of the water column as they approach their nearshore spawning areas. Based on these findings, lumpfish should be considered a semi-pelagic (or semi-demersal) fish. Lumpfish frequently exhibit demersal behaviour which warrants the use of the IGFS to monitor changes in population abundance. However, the variability in the behaviour between individuals makes it difficult to extend the lumpfish biomass index from the IGFS to absolute abundance.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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